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Comparison of the age and growth of red snapper (Lutjanus campechanus) amongst habitats and regions in the Gulf of Mexico

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COMPARISON OF THE AGE AND GROWTH OF RED SNAPPER (*LUTJANUS CAMPECHANUS*) AMONGST HABITATS AND REGIONS IN THE GULF OF MEXICO

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ABSTRACT

The Gulf of Mexico (GOM) red snapper stock has been exploited since the mid 1800s; yet it is still one of the most economically important fisheries in the GOM. Red snapper have been managed as a unit stock and are currently overfished, but perhaps no longer undergoing overfishing. Habitat varies greatly throughout the GOM and while numerous studies have aged red snapper, none have simultaneously compared the age and size structure and growth rates among standing and toppled oil and gas platforms with natural habitats. The objectives of this study were to examine the size and age structure and growth rates of red snapper among three different habitats (shelf-edge banks, standing platforms, toppled platforms) and six recreational fishing regions of the GOM (South Texas, North Texas, Louisiana, Alabama, Northwest Florida, Central Florida). Across all of the habitats and regions, red snapper were small (mean TL = 526.84 mm, mean TW = 0.97 kg) and from younger age classes (mean age = 4.44 yr), representing the strong recruitments of 2004, 2005 and 2006, with few fish older than seven years (1.5%). Total length, weight, and age frequencies, and growth models differed significantly among the habitats. Red snapper from the banks were significantly smaller at age and slower growing than red snapper from the artificial habitats. Also, shelf-edge banks appear to support a higher predominance of older red snapper compared to the artificial habitats. Demographic differences in red snapper size and age frequencies and growth parameters exist across the GOM. Small, fast-growing individuals dominated the recreational catches of South Texas, Northwest Florida, and Central Florida, whereas larger, slower growing red snapper constituted the majority of the Alabama and Louisiana catches. Also, both of the Florida regions' catches were comprised of significantly younger red snapper than catches in the north-central and western regions. To prevent habitat- and region-specific overfishing and promote stock recovery, these differences should be weighed when evaluating future stock assessments and management decisions. It is

also important for fisheries managers to note the absence of old red snapper in this study and its implications for the stock's recovery status.

CHAPTER 1: INTRODUCTION

To date, no studies have compared red snapper age and growth parameters between oil and gas platforms, low-relief artificial reefs, and natural hard bottom banks. While numerous studies have aged red snapper, none of these studies have examined red snapper from their natural habitat on shelf edge banks. Current knowledge of red snapper age and growth is based almost exclusively upon data from artificial habitats, which represent less than 5% of the suitable habitat in the GOM (Stanley and Wilson 2003), and fishery-dependent data, which are usually from undisclosed habitat types (Wilson and Nieland 2001; Nieland and Wilson 2003; SEDAR 2005). Without concrete information on the ecological function of natural habitats, it is impossible to address the debate over the quality, function, and influence of artificial reefs compared to their natural counterparts. To assess the efficacy of artificial habitat types as management tools, we need to know how the functional role that they play and how they contribute to existing information on vital population rates, such as growth and mortality. Also, population modeling, population assessments, and other management tools are reliant on accurate estimates of age and growth. This research specifically addresses the void in the baseline understanding of red snapper vital rates and helps define the biological reference points for this species on natural habitats.

1.1 Red Snapper

Red Snapper (*Lutjanus campechanus*) is one of the most economically and ecologically important reef fish species in the northern Gulf of Mexico (GOM). Red snapper are large, long-lived reef fish that inhabit the continental shelf from the Yucatan Peninsula, throughout the GOM, and into the western North Atlantic Ocean as far north as Cape Hatteras, North Carolina (Rivas 1966; Nelson and Manooch 1982; Hoese and Moore 1998). They can grow to be greater than 1000 mm total length (TL), 10 kg total weight, and can live for more than 50 years (Wilson and Nieland 2001; Allman and Fitzhugh 2007). Juvenile red snapper spend their first year or two on a variety of habitats on the inner-shelf, settling on mud/sand, shell habitats, small inshore reefs, and low-relief structure over mud/sand habitat (Workman and Foster 1994; Szedlmayer and Howe 1997; Szedlmayer and Conti 1999; Workman et al. 2002; Geary et al. 2007; Wells et al. 2008). Adult red snapper (age 2 – 9 yr) have a strong affinity for structure, inhabiting both natural hard-bottom (e.g. gravel bottoms, rock outcrops, reefs) and artificial habitats (e.g. artificial reefs, oil and gas platforms, shipwrecks) throughout the GOM (Moseley 1965; Bradley and Bryan 1975; Nelson and Manooch 1982; Szedlmayer and Shipp 1994; Gledhill 2001; Nieland and Wilson 2003; Wells and Cowan 2007).

Red snapper are batch spawners, and although they can reach sexual maturity early in life (~age 3 yrs), iteroparous females do not reach maximum spawning potential until age 12 – 15 yrs (Goodyear 1995; Render 1995; Woods et al. 2003; Jackson et al. 2007; Porch et al. 2007). Differences in maturation schedules have been reported for this species across the northern GOM, with red snapper from Alabama exhibiting signs of juvenescence, reaching maturity at younger ages and smaller sizes than those from Louisiana (Jackson et al. 2007). Juvenescence of a population is often cited as a compensatory response to fishing pressure or other environmental factors (Trippel 1995; Jackson et al. 2007). Red snapper have a protracted spawning season, lasting from May until September, with peak spawning occurring from June until August (Bradley and Bryan 1975; Render 1995; Woods et al. 2003; Jackson et al. 2007), with a spawning frequency of four to five days, giving an average female the potential to produce 12 to 20 batches of mature eggs per season (Render 1995; Woods et al. 2003; Jackson et al. 2006). The typical sex ratio observed in red snapper is nearly 1:1, which should allow for maximum spawning potential (Moseley 1965; Bradley and Bryan 1975; Patterson et al. 2001; Wilson and

Nieland 2001; Fischer et al. 2004; Nieland et al. 2007). After spawning, eggs and larvae remain in the plankton for an average of 30 days before they metamorphose and settle to benthic habitats (Szedlmayer and Conti 1999; Rooker et al. 2004).

Settlement of juveniles occurs as early as June and lasts through September (Rooker et al. 2004; Geary et al. 2007), on a variety of habitats ranging from open sand and mud to shell rubble and artificial structures (Workman and Foster 1994; Szedlmayer and Howe 1997; Szedlmayer and Conti 1999; Geary et al. 2007; Wells et al. 2008). Laboratory experiments have demonstrated that wild and hatchery-reared juvenile red snapper associate with artificial structure (Masuda et al. 2003) and shell habitats (Szedlmayer and Howe 1997). Several field studies support these findings, having found juvenile red snapper recruiting to low-relief artificial reef structures (Workman et al. 2002; Szedlmayer and Lee 2004) and shell banks (Szedlmayer and Conti 1999; Rooker et al. 2004; Geary et al. 2007). However, juvenile red snapper have also been found settled on open sand-mud habitat (Szedlmayer and Conti 1999; Rooker et al. 2004; Geary et al. 2007). Larger and older juveniles have been observed in greater abundance on ridge habitats and artificial structures (Szedlmayer and Conti 1999; Geary et al. 2007; Wells and Cowan 2007), with a void of one-year olds around offshore oil and gas platforms (Nieland and Wilson 2002); thus supporting the notion that red snapper recruit to higher-relief offshore, structured habitat as they mature. In fact, Bailey et al. (2001), based upon experiments in large tanks, found that adult conspecifics actively defend structure from juvenile settlement until a size refuge is reached when the juveniles are ~2 years old. Presumably, this is done to project juvenile from the “wall of mouths” on complex structured habitats. The ontogenetic shift in habitat is coupled with a diet shift, from smaller open-water prey like zooplankton, copepods, and small shrimp, to larger prey derived from surrounding sediments, such as mantis shrimp, squid, crabs, fish and shrimp (Moseley 1965; Bradley and Bryan 1975; Szedlmayer and Lee 2004; McCawley and Cowan 2007). Relatively little prey appear to be derived directly from the reefs (Moseley 1965; Bradley and Bryan 1975; McCawley and Cowan 2007).

1.2 Habitat

There are three general types of habitat in the continental shelf waters of the northern Gulf of Mexico: soft bottom (mud/sand/silt), natural hard bottom (shell rubble, rocky outcrops, reefs), and artificial hard substrate (oil platforms, ship wrecks, constructed reefs). The continental shelf across the GOM is predominantly soft bottom, with a mosaic of low-relief hard bottom and lined with shelf-edge banks offshore. It has been estimated that natural hard bottom habitat covers 1-3% of the northern GOM shelf, totaling about 2,800 km^2 (Parker et al. 1983), and covering up to 15% in some areas (Schroeder et al. 1995; Dufrene 2005). However, since the boom of oil exploration in the late 1940s, these waters now have an additional 12 km^2 of hard artificial structure (Stanley and Wilson 1997; Gallaway et al. 1998). There are about 3,500 oil and gas platforms in the GOM, forming the largest artificial reef complex in the world (Pulsipher et al. 2001). Most of the platforms are located on the continental shelf in the north-central and northwestern GOM (offshore of Mississippi, Louisiana and Texas). Even though this is a small proportion (<4%) of the total hard bottom habitat in the northwestern GOM, platforms may account for a biologically significant amount of artificial hard substrate on the shallow shelf.

The thousands of oil and gas platforms that line the northern GOM's continental shelf serve as 'de facto' artificial reefs, providing novel vertical habitat that connects the benthos to the photic zone (Stanley and Wilson 1990; Schroeder et al. 1995; Pulsipher et al. 2001). Platforms greatly influence the surrounding communities by providing substrate for epifaunal organisms, potentially increasing primary productivity and supporting various invertebrate and vertebrate communities and higher trophic levels (Gallaway et al. 1981; Render 1995), although recent evidence suggests that oil and gas platforms may be carbon sinks (Daigle 2011), much as Bortone et al. (1997) found for artificial reefs in the eastern GOM. Platforms also have the potential to increase the survival of the associated nekton communities by affording refuge from predation, increasing spawning substrate, and acting as a visual attractant (Gallaway et al. 1981). However, platforms may also function to greatly alter the assemblages in the local region and/or concentrate existing resources (Gallaway et al. 1981; Stanley and Wilson 2000). In addition, numerous species of fish congregate around platforms, making them a major destination for commercial and recreational fishermen (Reggio 1987; Stanley and Wilson 1990; Render and Wilson 1994; Gallaway et al. 1998; Stanley and Wilson 2000). Therefore, platforms can be sources of heavy exploitation, which in turn influence the surrounding community. It is assumed that oil and gas platforms have the potential to influence all life history stages of fishes inhabiting the coastal and continental shelf waters of the GOM. In spite of numerous investigations on the function of these large artificial habitats, their effects on the surrounding natural habitat and ecosystem in general remain poorly understood.

There is much debate and controversy over the impact of oil and gas platforms on the dynamics of many commercially and recreationally targeted fish species, specifically the attraction verses production hypotheses (Bohnsack 1989; Polovina 1989; Pickering and Whitmarsh 1997). The production hypothesis makes assumptions that red snapper are habitat limited, and states that artificial reefs and oil platforms provide additional critical habitat and increase the carrying capacity of the environment, thus increasing the biomass and abundance of fish; while the attraction hypothesis states that artificial reefs and oil platforms merely attract fish with behavioral preference for structure, and do not produce new biomass (Bohnsack 1989; Bohnsack et al. 1997; Grossman et al. 1997; Lindberg 1997; Bortone 1998; Cowan et al. 1999; Shipp 1999). If artificial reefs are indeed providing critical habitat and increasing biomass production, they should be considered as viable management tools. However, if they are simply attracting fish, they are most likely promoting overfishing. Several studies have attempted to address this question (Stanley and Wilson 1990; Hernandez and Shaw 2003; Rademacher and Render 2003; Lindquist et al. 2005; Wells and Cowan 2007), however, there is a lack of pre-platform data, and data from natural habitats.

Red snapper are known to be one of the most abundant reef fishes encountered at oil and gas platforms in the Gulf of Mexico (Gallaway et al. 1981; Stanley and Wilson 1990; Render 1995; Stanley and Wilson 2000; Nieland and Wilson 2003; Rademacher and Render 2003). It has been shown that juvenile and adult red snapper exhibit moderate site fidelity to the reefs they recruit to, with estimates ranging from 25% (Patterson et al. 2001; Patterson and Cowan 2003) to greater than 60% (Strelcheck et al. 2005; Szedlmayer and Schroepfer 2005) per year for artificial reefs. However, recent studies have shown red snapper to have high short-term fidelity to platforms, but low long-term fidelity, suggesting that platforms are mainly attraction devices (Westmeyer et al. 2007; McDonough 2009).

In the northern GOM, the shelf-edge banks off Louisiana are thought to be the primary natural habitats for red snapper, with red snapper accounting for up to 60% of the fish biomass (Gledhill 2001). These hard banks and rocky outcrops are common on the continental shelf throughout the GOM, covering a cumulative area of approximately 2800 km^2 (Parker et al. 1983; Rezak et al. 1985; Gledhill 2001). Unfortunately, current knowledge of red snapper age and growth, as well as most other life history and ecological characteristics, have been based upon data from the less prevalent artificial habitats. The limited age and size structure data available for red snapper from natural habitats is from vertical longline surveys in the western GOM on the Texas continental shelf (Mitchell et al. 2004) but not from the Louisiana continental shelf. Without a firm understanding of the functional role of natural habitats, it is impossible to address the debate over the quality, function, and influence of artificial reefs compared to their natural counterparts (Bohnsack 1989; Seaman 1997; Cowan et al. 2010).

1.3 Red Snapper Fisheries Management

The Gulf of Mexico red snapper stock has been exploited since the mid 1800s and is one of the most economically important fisheries in the GOM. However, this stock has been declining since the 1970s and is currently overfished (Goodyear 1995; SEDAR 2005; GMFMC 2007; Porch 2007; SEDAR 2009). The GOM red snapper fishery has multi-million dollar commercial and recreational sectors, and is also impacted by bycatch from the shrimp fishery.

Federal management of the red snapper fishery is required under the Magnuson-Stevens Fishery Conservation and Management Act (MSFCA). This management began relatively recently (starting in the late 1980s) and is controlled in federal waters by the National Marine Fisheries Service (NMFS) and the Gulf of Mexico Fishery Management Council (GMFMC) through the regulations they set in the Reef Fish Fishery Management Plan (Reef Fish FMP) and its amendments (GMFMC 1981). In 1989, the GMFMC established the red snapper rebuilding plan for the GOM stock, which reduced the commercial quota, set a bag limit for the recreational fishery, and set a goal of rebuilding the stock by the year 2000. Subsequent stock assessments and scientific research concluded that the condition of the fishery was far below the target and would not meet the 2000 goal; thus, several amendments were made to the quotas, bag limits, bycatch limits, and completion date. As of the 2004 red snapper stock assessment, the rebuilding goal was set to bring the red snapper stock to maximum sustainable yield by 2032, limiting the total allowable catch (TAC) at 5.0 million pounds (mp) between 2008 and 2010, making the commercial sector's quota 2.55 mp, leaving 2.45 mp to the recreational sector (GMFMC 2007; Hood et al. 2007). Results of the 2009 stock assessment update indicated that although the GOM red snapper stock is overfished, and that it is perhaps, no longer undergoing overfishing in the western GOM (GMFMC 2010). As a result, in 2011, the red snapper quotas were increased to 3.66 mp for the commercial sector and 3.525 mp for the recreational sector.

Red snapper management has been controversial due to the numerous sources of red snapper mortality. The commercial red snapper fishery and bycatch from the shrimp fishery are the main sources of fishing mortality in the western GOM, while the recreational fishery is the greatest source of fishing mortality in the eastern GOM (GMFMC 2007; SEDAR 2009). Therefore, management decisions must include considerations, alterations, and balance in regulations and goals between each of the three fisheries. Unfortunately, satisfying each fishery, as well as the law established in the MSFCA is extremely challenging, given political intentions, scientific uncertainty and time restrictions.

In 2007, the GMFMC implemented an individual fishing quota (IFQ) system for the commercial red snapper fishery to eliminate derby-style fishing and its associated problems, as well as give the fishermen incentive and long-term interest in the health and future of the stock (GMFMC 2006). The commercial fishery no longer has a set season, but it has a minimum harvestable size limit of 13 inches or greater (GMFMC 2007). The current policy for the recreational sector has reduced the recreational bag limit from 4 fish per person per day to 2 fish per person per day, with a 16 inch minimum size, and it has removed the captain and crew bag limits on for-hire vessels (GMFMC 2007). Along with the reduction in TAC and recreational bag limit came a necessary reduction in the recreational season, which is set from June 1st to September 30th; however, in 2009 NOAA Fisheries issued an early closure of August 15th and in 2011 the fishery will close on July 19th (GMFMC 2007; NMFS 2011). Also, to reduce red snapper and all finfish bycatch, shrimp trawl fishermen are required to have bycatch reduction devices (BRDs) on all shrimp trawl nets used in offshore waters. Originally, shrimp fishermen were required to reduce bycatch of juvenile red snapper by 50% of the 2001-2003 average. As of 2008, the shrimp trawl fishermen were required to reduce their red snapper bycatch by 74% from this average (GMFMC 2007). However, it has been shown that the BRDs are not extremely effective in reducing bycatch, with the potential to reduce shrimp trawl bycatch by 25-27% not 50-75% (Gallaway and Cole 1999). Red snapper bycatch in the shrimp fishery has declined in the past decade, partially due to the implementation of BRDs, but mainly due to the substantial decline of the shrimp industry in the GOM. The shrimp industry has declined substantially in size and effort since 2002 because of the rising costs of fuel, competition with low prices of imported shrimp, and damage from the major hurricanes of 2005 and 2008 (GMFMC 2007; SEDAR 2009). Estimated shrimping effort in 2008 showed a 74% decrease from the 2001-2003 baseline average (SEDAR 2009).

Even though red snapper in the GOM are currently managed as one unit stock, separate stock assessments have been conducted for sub-units east and west of the Mississippi River since 2004 (SEDAR 2005). Management under the unit stock hypothesis assumes no significant differences in red snapper population structure (genetics and life history characteristics) across the GOM. The unit stock assumption has been supported by early genetic analysis (Camper et al. 1993; Gold et al. 1997; Gold et al. 2001) as well as the capacity of red snapper to move great distances (Patterson et al. 2001). Also, in the past twenty years, two strong year classes (1989 and 1995) were found to dominate gulf-wide (Allman and Fitzhugh 2007), thus strengthening the unit-stock hypothesis. However, in the past decade, numerous studies have highlighted spatial differences in red snapper age and growth demographics in eastern versus western GOM red snapper (Allman et al. 2002; Fischer 2002; Fischer et al. 2004) as well as differences in red snapper maturation schedules across the GOM (Woods et al. 2003; Jackson et al. 2007). Recent population structure studies of red snapper genetics and movement suggest that GOM red snapper form a metapopulation of semi-isolated, distinct sub-populations (Saillant and Gold 2006; Gold and Saillant 2007; Patterson 2007). Examination of red snapper otolith microchemistry has also shown region-specific natural tags or 'elemental signatures,' which are being used to identify nursery sources, subpopulations, and stock mixing across the GOM (Patterson et al. 2008; Nowling et al. 2011; Sluis, personal communication[1]).

1.4 Red Snapper Age & Growth

Numerous studies have provided basic information on red snapper age and growth (Bradley and Bryan 1975; Nelson and Manooch 1982; Goodyear 1995; Render 1995; Manooch and Potts 1997; Patterson et al. 1998; Szedlmayer 1998; Patterson et al. 2001; Wilson and Nieland 2001; Nieland and Wilson 2003; Fischer et al. 2004; Allman and Fitzhugh 2007), and is typically accomplished by counting the opaque annuli (dark rings) along the ventral margin of the sulcus acousticus and marginal edge of sectioned otoliths (Nelson and Manooch 1982; Cowan et al. 1995). Otoliths are "earstones" that are composed of layers of calcium carbonate that are accreted throughout the fish's life. They are located beneath the brain in transparent inner ear canals and "float" in a viscous fluid-filled sac where they vibrate and move to stimulate

[1] Sluis, M. Z. 2011. Louisiana State University, Department of Oceanography and Coastal Sciences.

nerve fibers, which in turn aids in orientation and balance. Fish have three pairs of otoliths, sagittal, asteriscus and lapillus. The sagittal (the largest of the three) are the pair most frequently used to age fish. Nelson and Manooch (1982) first used sagittal otoliths to age red snapper in 1982, and since then the ageing and sectioning processes have been perfected and validated (Chang 1982; Nelson and Manooch 1982; Beamish and McFarlane 1983; Beckman et al. 1988; Cowan et al. 1995; Goodyear 1995; Baker and Wilson 2001; Fischer 2007; Szedlmayer and Beyer 2011). Ageing red snapper by otolith annuli counts was validated by radiocarbon dating methods, which has confirmed red snapper longevities of 50+ years (Baker and Wilson 2001).

One of the primary difficulties with using otoliths to age red snapper is the precision among readers. Because age estimation is subjective, precision is an important measure in assessing the reproducibility of age estimates between readers and laboratories (Campana 2001; Allman et al. 2005; Fischer 2007). A measurement of precision is also important when comparing the proficiencies of readers and assessing a reader's proficiency over time, and is key to increasing the performance of routine ageing facilities, especially for stock assessment purposes (Campana 2001; Allman et al. 2002; Allman et al. 2005). The two common measures of ageing precision are average percent error (APE) and coefficient of variation (CV) (Beamish and Fournier 1981; Campana 2001). The APE is an index of ageing precision, where smaller index values indicate increased precision (Beamish and Fournier 1981). A precision benchmark has been set at an APE of ″5% for long-lived species such as red snapper (Campana 2001; Allman et al. 2005). However, red snapper are fairly difficult to age (see precision levels from: (Render 1995; Wilson and Nieland 2001; Allman et al. 2002; Allman et al. 2005). The greatest source of error between readers comes from interpretation of the otoliths' edge and the first annulus (Wilson and Nieland 2001; Allman et al. 2005). Therefore, quality control during age estimation is needed to ensure standardization and increased precision of red snapper age estimates Gulf-wide.

In 2003, the Gulf States Marine Fisheries Commission (GSMFC) began holding annual ageing workshops to address the difficulties in ageing red snapper and other species, and the GSMFC produced a handbook guide for age determination of fishes of the GOM (Allman et al. 2005; VanderKooy 2009). In an attempt to increase the precision and standardization of red snapper age estimation, several studies have addressed the difficulties of edge interpretation and identification of the first annulus (Szedlmayer 1998; Patterson et al. 2001; Wilson and Nieland 2001; Allman et al. 2005; Mareska 2005; Fischer et al. 2010). Also in 2003, the National Marine Fisheries Service Panama City Laboratory (in conjunction with the GSMFC) assembled a red snapper otolith reference collection, which has been distributed to the main red snapper ageing laboratories in the Gulf of Mexico. The reference collection is used to identify the sources of ageing errors and calculate the APE between ageing laboratories (Allman et al. 2005). This reference collection is re-circulated annually to monitor precision and serve as an important training tool for red snapper ageing laboratories (Allman et al. 2005; Fischer 2007). This important quality control monitoring system has helped improve the precision in red snapper ageing Gulf-wide (Allman et al. 2005).

Most red snapper age and growth studies have focused on samples from the commercial and recreational fisheries. The collection of dockside samples from the recreational and commercial fisheries has allowed scientists and managers to better understand catch-at-age of the population (Nelson and Manooch 1982; Allman and Fitzhugh 2007; Nieland et al. 2007; Nieland et al. 2007). However, an assortment of ageing techniques (e.g. scales, whole otoliths, sectioned otoliths, and length frequencies) has been used to age these samples, making it difficult to compare age structure and maximum longevity. Comparison of ageing studies is also difficult because the variety of sources (e.g. commercial fishery, recreational fishery, fishery-independent survey) and locations from which the samples were collected may bias the observed age structure.

Originally, red snapper were thought to reach 10 to 20 years of age, based upon readings from scales and length frequencies (Futch and Bruger 1976; Nelson and Manooch 1982). The validation and use of transverse otolith sections for ageing red snapper greatly increased the estimated maximum longevity of red snapper to ranging from 53 to 57 years (Render 1995; Wilson and Nieland 2001; Allman and Fitzhugh 2007). It is interesting to note that differences have been found between the age ranges harvested by the commercial and recreational fisheries across the GOM. In the early 1990s, the oldest red snapper sampled were from the commercial fishery in Louisiana, with several fish older than 20 years, while the samples from the recreational sector did not contain fish older than 22 years (Render 1995). A subsequent study spanning 12 years and the entire US waters of the GOM also found that the recreational fishery had a lower mean age (3.2 years) than both the commercial vertical hook and line fishery (4.1 years) and the commercial longline fishery (7.8 years) (Allman and Fitzhugh 2007). Wilson and Nieland (2001) also examined a lengthy data set of red snapper collected from the recreational and commercial fisheries in Louisiana and eastern Texas dating from 1989 to 1992 and from 1995 to 1998. They examined 3,791 otoliths, and estimated ages ranged from 0.5 to 52.6 years corresponding to lengths of 104 to 1039 mm and weights of 0.02 to 22.79 kg (Wilson and Nieland 2001).

The size at age of red snapper caught in Louisiana’s commercial fishery has declined significantly in the past decade (Nieland et al. 2007). From 2001 to 2004, the mean size of four year old red snapper declined from 525 to 445 mm, five year olds declined from 590 to 475, and six year olds from 692 to 507 mm (Nieland et al. 2007). This decline in size at age may be the result of overexploitation, where the vast majority of red snapper are being harvested young, close to the minimum total length regulations (Nieland et al. 2007).

In the past decade, a significant difference between the age-frequency distributions and size-at-age of red snapper across the northern GOM has been observed (Allman et al. 2002; Fischer 2002; Fischer et al. 2004). Fischer et al. 2004 found Texas red snapper (sampled from the recreational catch) reached smaller maximum size at a faster rate than Louisiana and Alabama red snapper; the majority of Texas red snapper were under three years old and 375 mm fork length. In spite of this regional growth difference, all red snapper had similar growth curves, with rapid growth through age 8 to 10 years (Fischer et al. 2004). Corresponding to Fischer et al's findings, Saillant and Gold (2006) found the population structure of red snapper to vary across the GOM, indicating different "demographic stocks" with dramatically different effective population sizes (Saillant and Gold 2006). These findings may be due to a combination of differing environmental conditions and management regimes across the northern GOM as well as the type of recreational fishing (headboats in Texas versus charter boats in Louisiana and Alabama) and the disproportionately high discard-to-landing ratio reported for headboats in Texas (Fischer et al. 2004). The distribution of fishing sectors (a high proportion of the commercial landings come from the western GOM and the majority of the recreational landings occur in the eastern GOM) and their differing management plans may also influence the formation of demographic stocks. The most recent findings indicate that red snapper across the northern GOM form a metapopulation (or network) of semi-isolated assemblages that are demographically distinct but also highly influenced by migration between assemblages (Gold and Saillant 2007; Patterson 2007).

While numerous studies have used otoliths to age red snapper and provide growth information, very few have examined red snapper from their natural habitat on shelf edge banks. Mitchell (2004) examined the age structure red snapper caught on research longlines along the Texas shelf edge, however, this was a gear-specific study. Previous red snapper age and growth studies have focused on inshore artificial reefs (Render 1995; Patterson et al. 2001; Wilson and Nieland 2001; Fischer et al. 2004) and red snapper from unknown locations by dockside sampling of the recreational and commercial fisheries (Bradley and Bryan 1975; Nelson and Manooch 1982; Manooch and Potts 1997; Wilson and Nieland 2001; Fischer et al. 2004; Allman and Fitzhugh 2007; Nieland et al. 2007; Nieland et al. 2007). The sampling bias associated with artificial habitats is likely related to their close proximity to shore, they are easier to locate than natural habitats, and red snapper are abundant on artificial reefs. Recently, the oldest red snapper from an artificial reef system off the coast of Alabama was found to be 34.1 yr old, however, the majority of the catch was between the ages of two and eight, with growth rates slowing around seven to nine yr of age (Patterson et al. 2001). While the female to male ratio was a normal 1:1 for the red snapper sample overall, females dominated the older (>10 years) age classes from this artificial reef system (Patterson et al. 2001). Currently, we are unable to compare these findings to those of red snapper from natural habitats, because there is a paucity of age and growth data of red snapper that is definitely from natural reefs. There is great concern regarding this lack of information in our basic understanding of the ecology and life history of red snapper, as well as the importance of natural habitat to the production and sustainability of the fishery.

1.5 Thesis Goals and Objectives

The objective of this study was to examine the size and age structure and growth rates of red snapper among different habitats and regions of the Gulf of Mexico. In chapter 2, I estimated and compared the size and age structure, growth models, and size-at-age of red snapper from offshore natural habitats, standing oil and gas platforms, and toppled oil and gas platforms. This research was part of a collaborative project attempting to better understand the role that natural reefs play in the ecology and demographics of red snapper in the GOM. This project was particularly interested in comparing the relative benefits of natural reefs to artificial reefs for red snapper. In chapter 3, I estimated and compared the size and age structure, growth models, and size-at-age of red snapper from six recreational fishing regions across the GOM in order to elucidate the trends in the demographic differences noted in the most recent red snapper stock assessments and research studies. Overall, this research will help address the critical need for understanding the role of natural habitats in the life history and ecology of red snapper in the northern GOM as well as elucidate trends in region-specific age and growth information needed to further evaluate the need for management sub-units.

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CHAPTER 2: HABITAT-SPECIFIC DIFFERENCE IN RED SNAPPER (*LUTJANUS CAMPECHANUS*) AGE AND GROWTH IN THE NORTHERN GULF OF MEXICO

2.1 Introduction

To date, no studies have compared simultaneously red snapper (*Lutjanus campechanus*) age and growth parameters between oil and gas platforms, low-relief artificial reefs, and natural hard bottom banks. While numerous studies have aged red snapper, none of these studies have examined red snapper from their natural habitat on shelf-edge banks. Current knowledge of red snapper age and growth is based almost exclusively upon data from artificial habitats, which represent less than 5% of the suitable habitat in the GOM (Stanley and Wilson 2003), and fishery-dependent data, which are usually from undisclosed habitat types (Wilson and Nieland 2001; Nieland and Wilson 2003; Fischer et al. 2004; SEDAR 2005). Without concrete information on the ecological function of natural habitats, it is impossible to address the debate over the quality, function, and influence of artificial reefs compared to their natural counterparts. To assess the efficacy of artificial habitat types as management tools, we need to know the functional role that they play and how they contribute to existing information on vital population rates, such as growth and mortality. Also, population modeling, stock assessments, and other management tools are reliant on accurate estimates of age and growth. This research specifically addresses the void in the baseline understanding of red snapper vital rates and helps define the biological reference points for this species on natural habitats.

Red snapper are large, long-lived reef-associated fish that inhabit the continental shelf from the Yucatan Peninsula, throughout the GOM, and into the western North Atlantic Ocean as far north as Cape Hatteras, North Carolina (Rivas 1966; Nelson and Manooch 1982; Hoese and Moore 1998). They can grow to be greater than 1000 mm total length (TL), 10 kg total weight, and can live for more than 50 yr (Wilson and Nieland 2001; Allman et al. 2009). Juvenile red snapper spend their first year or two on a variety of habitats on the inner-shelf, settling on shell habitats, small inshore reefs, and low relief structure over sand habitat (Workman and Foster 1994; Szedlmayer and Howe 1997; Szedlmayer and Conti 1999; Workman et al. 2002; Geary et al. 2007; Wells et al. 2008). Adult red snapper have a strong affinity for structure, inhabiting both natural hard-bottom (e.g. gravel bottoms, rock outcrops, reefs) and artificial habitats (e.g. artificial reefs, oil and gas platforms, shipwrecks) throughout the GOM (Moseley 1965; Bradley and Bryan 1975; Nelson and Manooch 1982; Szedlmayer and Shipp 1994; Gledhill 2001; Nieland and Wilson 2003; Wells and Cowan 2007). Red snapper are known to be one of the most abundant reef fishes encountered at oil and gas platforms in the Gulf of Mexico (Gallaway et al. 1981; Stanley and Wilson 1990; Render 1995; Stanley and Wilson 2000; Nieland and Wilson 2003; Rademacher and Render 2003). It has been shown that juvenile and adult red snapper exhibit moderate site fidelity to the reefs they recruit to, with higher short-term fidelity and lower long-term fidelity, decreasing both with time and fish age (Patterson et al. 2001; Patterson and Cowan 2003; Strelcheck et al. 2005; Szedlmayer and Schroepfer 2005; Peabody and Wilson 2006; Westmeyer et al. 2007; McDonough 2009).

There are three general types of habitat in the continental shelf waters of the northern Gulf of Mexico: soft bottom (mud/sand/silt), natural hard bottom (shell rubble, rocky outcrops, reefs), and artificial hard substrate (oil platforms, ship wrecks, constructed reefs). It has been estimated that natural hard bottom habitat covers 1-3% of the northern GOM shelf, totaling about 2,800 km^2 (Parker et al. 1983), and covering up to 15% in some areas (Schroeder et al. 1995; Dufrene 2005). The northern GOM is predominantly soft bottom, with a mosaic of low-relief hard bottom, and lined with shelf-edge banks offshore. However, since the boom of oil exploration in the late 1940s, these waters now have an additional 12 km^2 of hard artificial structure (Stanley and Wilson 1997; Gallaway et al. 1998). There are about 3,500 oil and gas platforms in the GOM, which form the largest artificial reef complex in the world (Pulsipher et al. 2001). Most of the platforms are located on the continental shelf in the north-central and northwestern GOM (offshore of Mississippi, Louisiana and Texas). Even though this is a small proportion (<4%) of the total hard substrate in the northwestern GOM, platforms may account for a biologically significant amount of artificial hard substrate on the shallow shelf.

The thousands of oil and gas platforms that line the northern GOM's continental shelf serve as 'de facto' artificial reefs, providing novel vertical habitat that connects the benthos to the photic zone (Stanley and Wilson 1990; Gallaway et al. 1998). Platforms greatly influence the surrounding communities by providing substrate for epifaunal organisms, potentially increasing primary productivity and supporting various invertebrate and vertebrate communities and higher trophic levels (Gallaway et al. 1981; Render 1995). Platforms also have the potential to increase the survival of the associated nekton communities by affording refuge from predation, increasing spawning substrate, and acting as a visual attractant (Gallaway et al. 1981), although recent evidence suggests that oil and gas platforms may be carbon sinks (Daigle 2011). However, platforms may also function to greatly alter the assemblages in the local region and/or concentrate existing resources (Gallaway et al. 1981; Stanley and Wilson 2000). In addition, numerous species of sportfish congregate around platforms, making them a major destination for commercial and recreational fishermen (Reggio 1987; Stanley and Wilson 1990; Render and Wilson 1994; Gallaway et al. 1998; Stanley and Wilson 2000). Therefore, platforms can be sources of heavy exploitation, which in turn influence the surrounding community. It is assumed that oil and gas platforms have the potential to influence all life history stages of fishes inhabiting the coastal and continental shelf waters of the GOM. In spite of numerous investigations on the function of these large artificial habitats, their effects on the surrounding natural habitat and ecosystem in general remain poorly understood.

There is much debate and controversy over the impact of oil and gas platforms on the dynamics of many commercially and recreationally targeted fish species, specifically the attraction verses production hypotheses (Bohnsack 1989; Pickering and Whitmarsh 1997). The production hypothesis makes assumptions that red snapper are habitat limited, and states that artificial reefs and oil platforms provide additional critical habitat and increase the carrying capacity of the environment, thus increasing the biomass and abundance of fish; while the attraction hypothesis states that artificial reefs and oil platforms merely attract fish with behavioral preference for structure, and do not produce new biomass (Bohnsack 1989; Bohnsack et al. 1997; Grossman et al. 1997; Lindberg 1997; Bortone 1998; Cowan et al. 1999; Shipp 1999; Cowan et al. 2010). If they are indeed providing critical habitat and increasing biomass production, they should be considered as viable management tools. However, if they are simply attracting fish, they are most likely promoting overexploitation. Several studies have attempted to address this question (Stanley and Wilson 1990; Hernandez and Shaw 2003; Rademacher and Render 2003; Lindquist et al. 2005; Wells and Cowan 2007; Gallaway et al. 2009; Cowan et al. 2010) however, there is a lack of pre-platform data, and data from natural habitats.

In the northern Gulf of Mexico, the shelf-edge banks off Louisiana are thought to be the primary natural habitats for red snapper, with red snapper accounting for up to 60% of the fish biomass (Gledhill 2001). These hard banks and rocky outcrops are common on the continental shelf throughout the GOM, covering a cumulative area of approximately 2800 km^2 (Parker et al. 1983; Rezak et al. 1985; Gledhill 2001). Unfortunately, current knowledge of red snapper age and growth, as well as most other life history and ecological characteristics, have been based upon data from the less prevalent artificial habitats. The limited age and size structure data available for red snapper from natural habitats is from vertical longline surveys in the western GOM on the Texas continental shelf (Mitchell et al. 2004) but not from the Louisiana continental shelf. Without a firm understanding of the functional role of natural habitats, it is impossible to address the debate over the quality, function, and influence of artificial reefs compared to their natural counterparts (Bohnsack 1989; Seaman 1997; Cowan et al. 2010).

2.2 Methods

Red snapper were collected from three types of habitat in the northwestern Gulf of Mexico during the summers of 2009 and 2010. The three types of habitat were natural hard-bottom shelf-edge banks (banks), standing oil and gas platforms (standing platforms), and toppled oil and gas platforms (toppled platforms), located in similar water depths on Louisiana's outer continental shelf (Fig 2.1). Red snapper were collected with vertical longlines, baited chevron fish traps, and otter trawls. The vertical longlines were constructed based upon the specifications of the gear to be used during a NMFS survey on 250 oil and gas platforms throughout the GOM. Eight baited chevron traps, of standard MARMAP chevron configuration (dimensions = 150 cm width x 180 cm length x 60 cm height; opening = 44.5 cm x 10 cm; mesh = 3.8 plastic coated wire), were deployed for two hours at 0.5 km intervals north and south of each platform and at random distances across the banks. For all fish collected, morphometric measurements were recorded (total length [TL] in millimeters and total weight [TW] in grams), sex was determined by macroscopic examination of gonads, and sagittal otoliths were removed, rinsed, and stored in coin envelopes until processed.

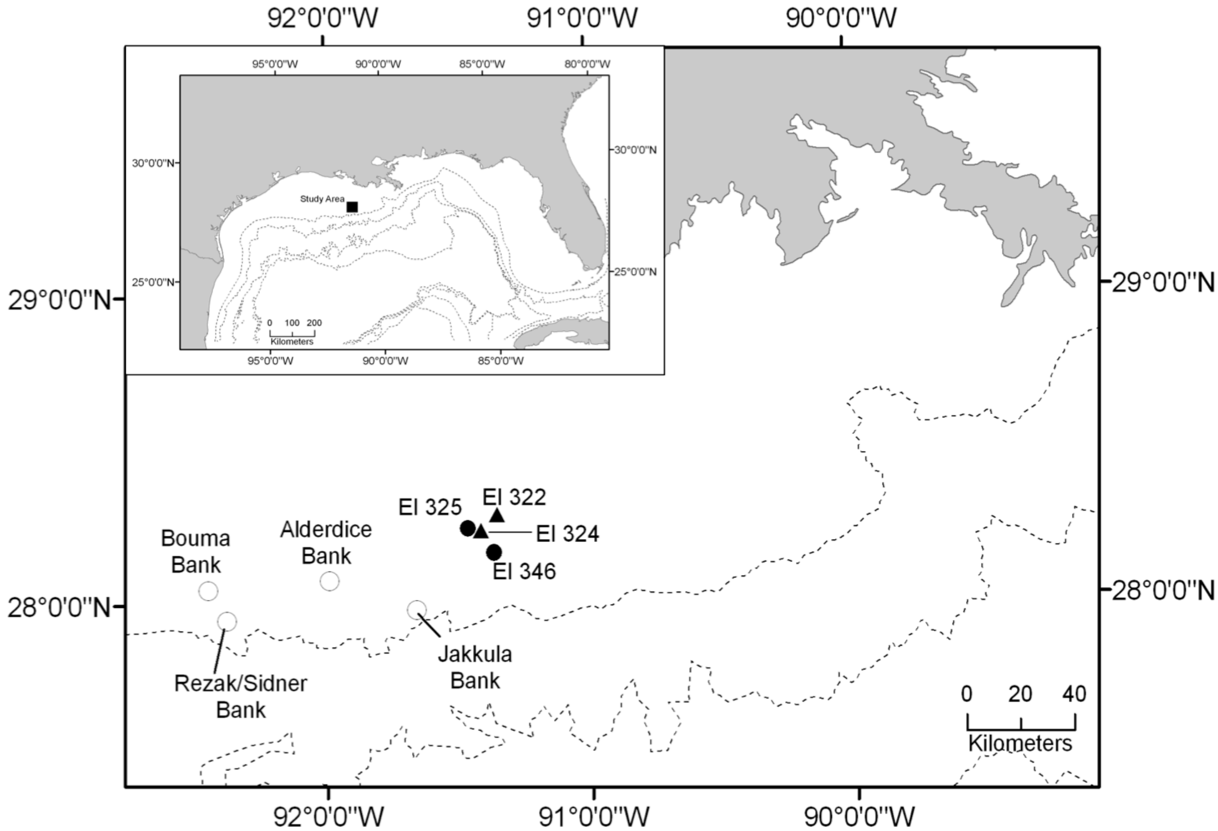

Figure 2.1. Map of the red snapper (*Lutjanus campechanus*) sampling locations on the Louisiana continental shelf in the northwestern Gulf of Mexico. Open circles denote shelf-edge banks, dark circles represent standing platforms, and triangles denote toppled platforms. Contour lines represent depths of 200m, 1000m, 2000m, and 3000m. Map courtesy of K. M. Boswell.

2.2.1 Otolith Processing and Aging

The left sagittal otoliths were sectioned in the transverse plane following the methods of Cowan et al. (1995). Sections were made using the Hillquist model 800 thin-sectioning machine equipped with a diamond embedded wafering blade and precision grinder (Cowan et al. 1995). When the left otoliths were unavailable or damaged, the right otoliths were sectioned. Otolith sections were read under a dissecting microscope with transmitted light and a polarized light filter at 20x to 64x magnification. Counts of opaque annuli were made along the ventral margin of the sulcus acousticus from the core to the proximal edge (Wilson and Nieland 2001). The appearance of the otolith's margin, known as edge condition, was coded according to Beckman et al. (1988). Annulus counts were performed by two independent readers without knowledge of date or location of capture or morphometric data. When initial counts disagreed, annuli were counted a second time. In instances where a consensus between the two readers could not be reached, the annulus counts from the more experienced reader were reported. Precision between readers was evaluated with the coefficient of variation (CV), index of precision (D) (Chang 1982), and average percent error (APE) (Beamish and Fournier 1981). Ages of red snapper were estimated from the number of opaque annuli, assumed birthdate, and capture date, following the equation described by Wilson and Nieland (2001):

$$\text{Age (days)} = -182 + (\textit{annulus count} \times 365) + ((m-1) \times 30) + d, \quad (1)$$

where m = the ordinal number (1-12) of month of capture; and d = the ordinal number (1- 31) of the day of the month of capture. It was assumed for red snapper in the northern Gulf that annulus formation begins on 1 January, with a uniform birthdate of 1 July. To account for the uniform birthdate, 182 days were subtracted from each age estimate. To assign a biological age in years, the age in days was divided by 365.

2.2.2 Size and Age Distributions

Analysis of variance (ANOVA) models were used to compare mean total length (TL), total weight (TW), and age among habitats (SAS Institute 2008). Total length, TW, and age were first ln-transformed to meet the assumptions of normality and homogeneity of variance. Tukey's Studentized Range (HSD) Test was used for pair-wise comparison of means. Size and age distributions were compared pair-wise by habitat with the Kolmogorov-Smirnov two-sample test. A chi-squared (χ^2) test was used to determine if sex ratios differed from 1:1 overall and among habitats. For all statistical tests, significance was measured at an alpha level of 0.05.

2.2.3 Growth

Traditional allometric relationships of fish length to weight were fitted with linear regression to the model TL = aTW^b from ln-transformed data for all fish combined and by habitat. Analysis of Covariance (ANCOVA) was used to compare, among habitats, the linearized slopes and intercepts, corresponding to the exponent b and multiplier a in the exponential length-weight model. For all statistical tests, significance was measured at an alpha level of 0.05.

To examine growth differences among red snapper from the three habitat types, weighted mean size-at-age was compared for the most common ages (3-6 yr) using ANOVA with a Tukey's Studentized (HSD) Adjustment for post-hoc comparisons. Several models were applied to compare red snapper growth rate among the habitats. For all ages sampled, observed TL at age and TW at age were modeled with the von Bertalanffy growth equations. For all von Bertalanffy equations, no y-intercepts for t_0 were specified and models were forced through 0 for comparison purposes due to a lack of individuals younger than 2 yr in all sample populations. Von Bertalanffy growth models were fitted with nonlinear regression by least squares (SAS Institute 2008) in the forms:

$$TL_t=L_\infty(1-e^{-k(t)}) , \qquad (2)$$

$$TW_t=W_\infty (1-e^{-k(t)})^b , \qquad (3)$$

where: TL_t = TL at age t; L_∞ = the TL asymptote;

TW_t = TW at age t; W_∞ = the TW asymptote;

k = the growth coefficient; t = age in yr;

b = exponent derived from the length-weight regressions.

Growth rates were also modeled with linear regression fitted to observed TL at age and TW at age for ages 1-7, which was the period of rapid growth of red snapper observed in this study. Growth models were calculated for all red snapper combined and separately by habitat and sex. Linear growth models were compared among habitats with ANCOVA and tested for homogeneity of slopes and intercepts. Likelihood ratio tests (Cerrato 1990) were used to test for differences among habitats in von Bertalanffy models and in growth parameter estimates using the solver function in Microsoft Excel 2008 (Haddon 2001). For all statistical tests, significance was measured at an alpha level of 0.05.

2.3 Results

During the summers of 2009 and 2010, 582 red snapper from three different types of habitat on Louisiana's continental shelf were sampled for morphometric data and sagittal otoliths (Table 2.1): 256 specimens from banks, 204 specimens from standing platforms, and 121 specimens from toppled platforms. The samples included 313 females, 256 males, and 12 individuals of unknown sex (Table 2.1). The resultant male-to-female ratios were 0.63:1 for banks, 0.90:1 for standing platforms, 1:0.82 for toppled platforms, and 0.82:1 for all habitats combined. A chi-square test indicated no significant difference in the number of males to females for the standing and toppled platforms (χ^2 =0.51, p=0.475 and χ^2 =1.20 p=0.273, respectively). The chi-square test indicated a significantly greater number of females than males from the banks (χ^2 =13.24 p=0.0003). However, this selectively should not affect the results, as previous studies have not found a significant difference between male-to-female ratios in the population nor between male and female size (Wilson and Nieland 2001; Fischer et al. 2004). No significant differences were found between the TL-TW regression models for the males and females (ANCOVA test of homogeneity of slopes, $F_{1,576}$=0.26; p=0.7686; r^2=0.97; ANCOVA test of equal intercepts, $F_{1,576}$=0.43; p=0.6504; r^2=0.97).

2.3.1 Size and Age Distributions

Total lengths of all red snapper sampled ranged from 141 to 987 mm with a mean of 486.43 ± 4.16 mm (Fig 2.2A). Red snapper from the banks ranged from 244 to 807 mm TL with a mean of 462.44 ± 5.85 mm, which was significantly smaller than the mean TL of red snapper from the standing platforms (mean TL = 496.10 ± 7.59 mm, Tukey's test: $p=0.0024$) and from the toppled platforms (mean TL = 520.86 ± 7.89 mm, Tukey's test: $p<0.0001$) (Fig 2.3A). Red snapper from the standing platforms ranged from 141 to 818 mm TL, and red snapper from the toppled platforms ranged from 197 to 987 mm TL (Fig 2.3A). On average, red snapper from the toppled platforms were significantly longer than red snapper from the standing platforms (Tukey's test: $p=0.0306$) and the banks (Tukey's test: $p<0.0001$). The total length frequency distributions of the samples were significantly different among the habitats (Banks vs. Standing P>KSa: $p<0.0001$; Banks vs. Toppled P>KSa: $p<0.0001$; Standing vs. Toppled P>KSa: $p=0.0009$). The toppled platforms had the highest proportion of larger individuals; 59.5% of sampled red snapper from toppled platforms were 550 mm or longer, compared to 42.2% of the red snapper sampled from the standing platforms and 27.3% of the red snapper sampled from the banks (Fig 2.3A).

Table 2.1. Numbers of red snapper, *Lutjanus campechanus*, sampled from Louisiana's continental shelf by habitat type.

Habitat Type	Males	Females	Unknown Sex	Total
Banks	97	156	3	256
Standing Platforms	93	103	8	204
Toppled Platforms	66	54	1	121

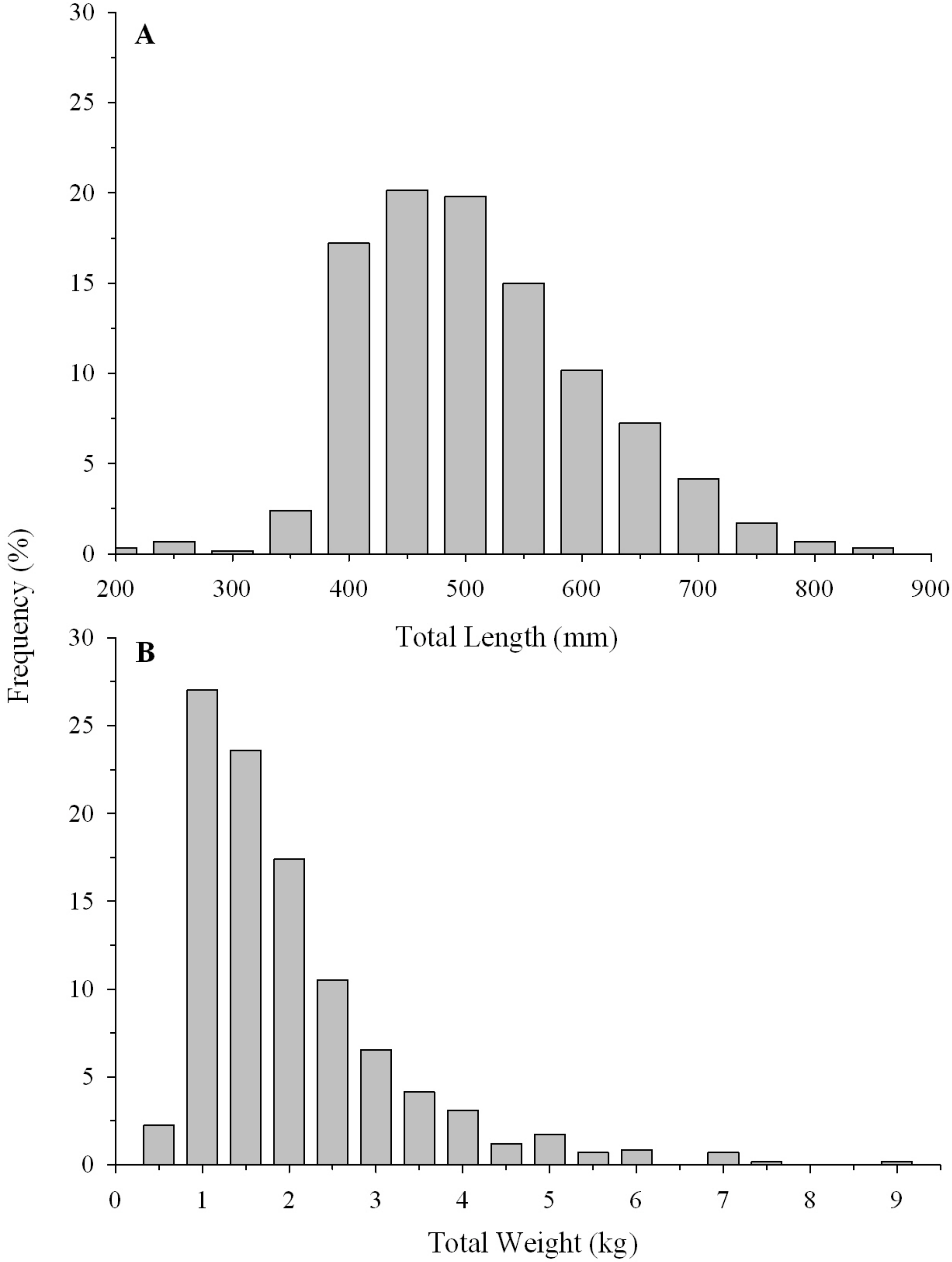

Figure 2.2. Distributions of (A) total length in mm and (B) total weight in kg for red snapper, *Lutjanus campechanus*, sampled from Louisiana's continental shelf (n=582).

Total weights ranged from 0.11 to 8.71 kg with a mean of 1.76 ± 0.05 kg (Fig 2.2B). Red snapper from the banks ranged from 0.33 to 7.07 kg TW with a mean of 1.46 ± 0.07 kg, which was significantly smaller than the mean TW of red snapper from the standing platforms (mean TW = 1.94 ± 0.09 kg, Tukey's test: $p<0.0001$) and the toppled platforms (mean TW = 2.08 ± 0.10 kg, Tukey's test: $p<0.0001$) (Fig 2.3B). The red snapper from the standing platforms ranged from 0.11 to 8.71 kg, and red snapper from the toppled platforms ranged from 0.11 to 6.58 kg (Fig 2.3B). On average, red snapper from the toppled platforms were significantly heavier than red snapper from the banks (Tukey's test: $p<0.0001$), but not from red snapper from the standing platforms (Tukey's test: $p=0.0958$). The total weight frequency distributions of the samples were significantly different between all three habitats (Banks vs. Standing P>KSa: $p<0.0001$; Banks vs. Toppled P>KSa: $p<0.0001$; Standing vs. Toppled P>KSa: $p=0.0044$). The banks had a much lower proportion of larger individuals; 13.7% of the fish sampled from the banks were 3.0 kg or heavier, compared to 24.5% of the fish sampled from the standing platforms and 22.3% of the sampled fish from the toppled platforms (Fig 2.3B).

Significant differences in red snapper TL-TW regression models were detected among the habitats (ANCOVA test of homogeneity of slopes, $F_{2, 575}=6.63$; $p=0.0014$; $r^2=0.976$; ANCOVA test for equal intercepts, $F_{2, 575}=7.95$; $p=0.0004$; $r^2=0.976$); therefore separate models were fitted for each habitat (Fig 2.4). The resultant TW-TL equations are given in Table 2.2.

Table 2.2. Total weight – total length regression models for red snapper, *Lutjanus campechanus*, sampled from three habitats on Louisiana's continental shelf.

Site	TW-TL equation	df	F	p-value	r^2
All Data	$TW = 1.71x10^{-8}(TL^{2.96})$	579	19300.00	<0.0001	0.971
Banks	$TW = 1.17x10^{-8}(TL^{3.02})$	254	8612.17	<0.0001	0.971
Standing	$TW = 3.41x10^{-8}(TL^{2.86})$	202	10448.5	<0.0001	0.981
Toppled	$TW = 2.27x10^{-8}(TL^{2.92})$	119	2917.41	<0.0001	0.961

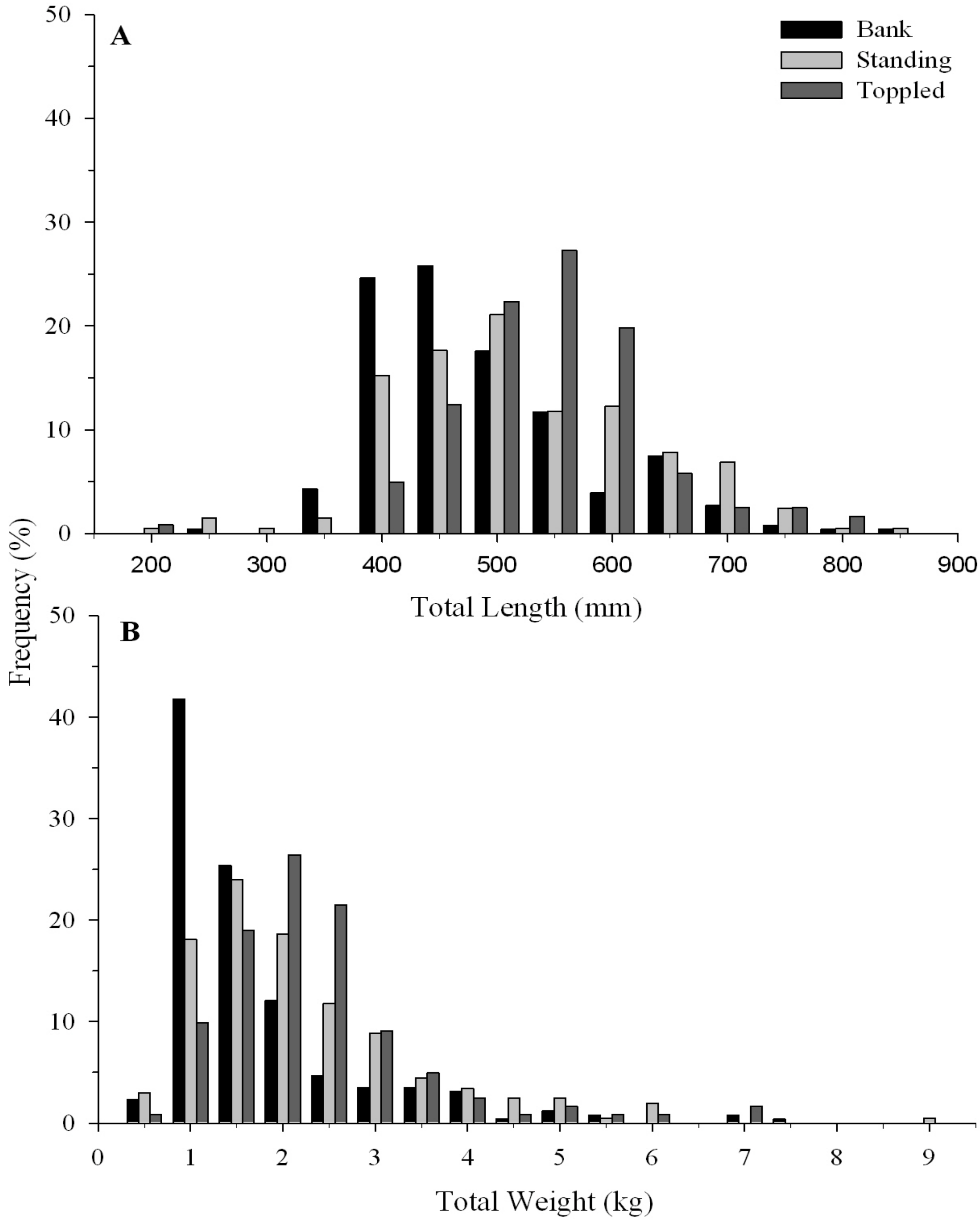

Figure 2.3. Distributions of (A) total length in mm and (B) total weight in kg for red snapper, *Lutjanus campechanus*, sampled from shelf-edge banks (n=256), standing platforms (n=204), and toppled platforms (n=121) on Louisiana's continental shelf.

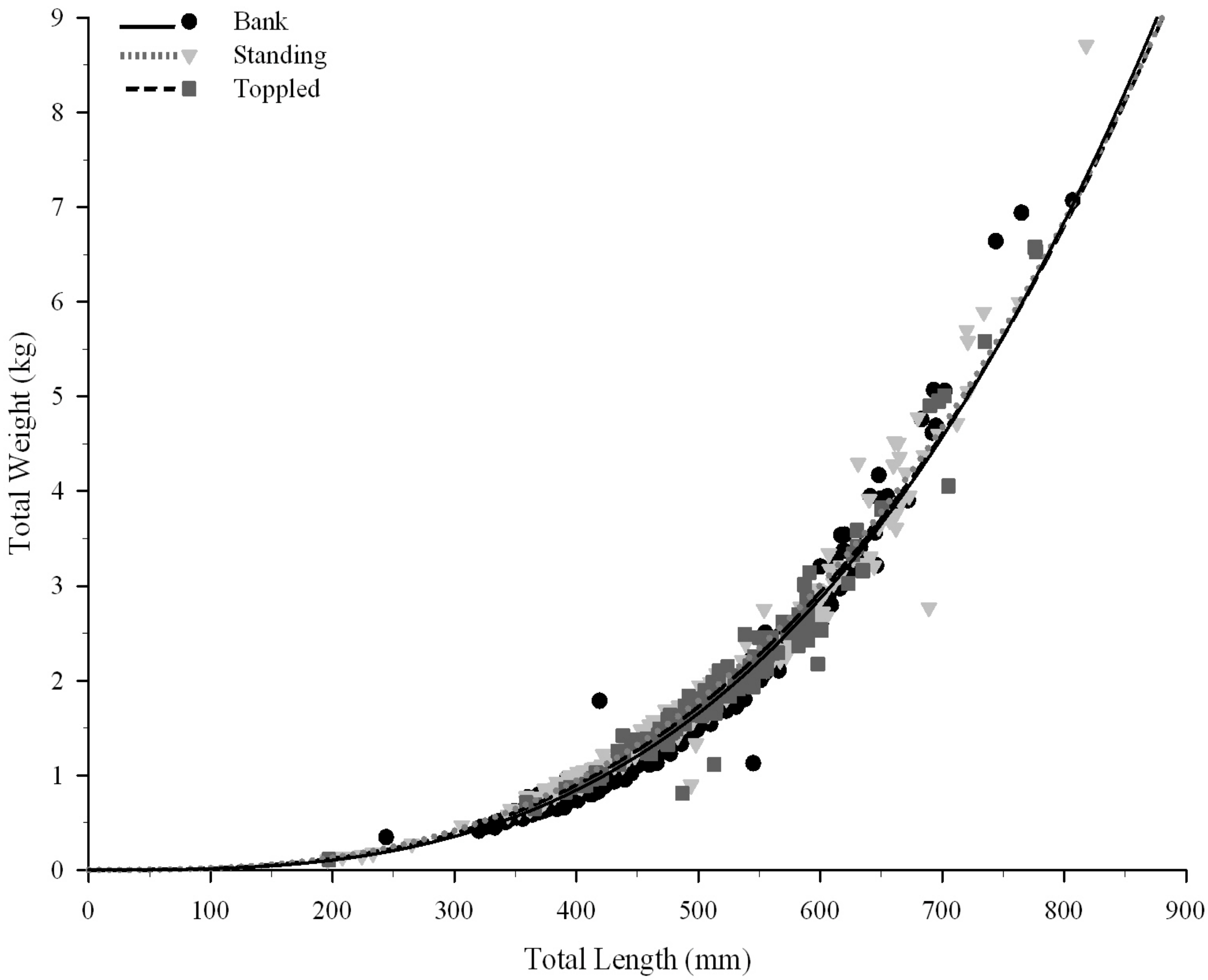

Figure 2.4. Scatterplot of the relationships between observed total weight (kg) and total length (mm) of red snapper, *Lutjanus campechanus*, from shelf edge banks (n=256), standing platforms (n=204), and toppled platforms (n=121) on Louisiana's continental shelf. Plotted lines represent the power functions fitted to the data from each habitat.

The TWL-TL equation for red snapper from the banks had a significantly larger growth coefficient (*b*) and a significantly smaller intercept (*a*) than the equation for red snapper from the standing platforms ($p=0.0002$ and $p<0.0001$, respectively). No significant differences occurred between the TW-TL parameters *b* and *a* for red snapper from the banks and toppled platforms ($p=0.0989$ and $p=0.0855$, respectively). Also, no significant differences occurred between the

TW-TL parameters *b* and *a* for red snapper from the standing and toppled platforms (p=0.3006 and p=0.2583, respectively).

Ages were obtained from 582 transverse otolith sections. After the initial reading, the two readers agreed on 63.7% of the otoliths, with an APE of 7.08% (Table 2.3). After the second reading, the readers reached agreement for 88.3% of otoliths, with an APE of 1.95% (Table 2.3). Ages of red snapper ranged from 1 to 21 yr, with the majority (90%) of individuals between 3 and 6 yr old (Fig 2.5A). Overall, the mean age was 4.23 ± 0.07 yr with relatively few (3%) red snapper aged older than seven yr (Fig 2.5A). The majority of the red snapper across all three habitats appear to be derived from the strong 2004, 2005 and 2006 year-classes (Fig 2.5B).

Table 2.3. Differences between the two readers in average percent error (APE), coefficient of variation (CV), index of precision (D), percentages of agreement (O) for opaque annuli counts, and percentages of differences in age estimates (±1, 2, and 3 or more yr) in red snapper, *Lutjanus campechanus*, otoliths after the first and second readings (n=582).

	1^{st} reading	2^{nd} reading
APE	7.078	1.954
CV	0.071	0.020
D	0.050	0.014
O	63.76%	88.38%
±1	28.55%	9.23%
±2	4.62%	1.71%
≥ ±3	3.07%	0.68%

Red snapper from the banks ranged from 2 to 11 yr with a mean age of 4.32 ± 0.09 yr (n=256) (Fig 2.6). Red snapper from the standing platforms ranged from 1 to 21 yr with a mean age of 4.10 yr ± 0.14 (n=204), and red snapper from the toppled platforms ranged from 1 to 12 yr with a mean age of 4.17 ± 0.11 yr (n=121) (Fig 2.6). On average, the red snapper collected at

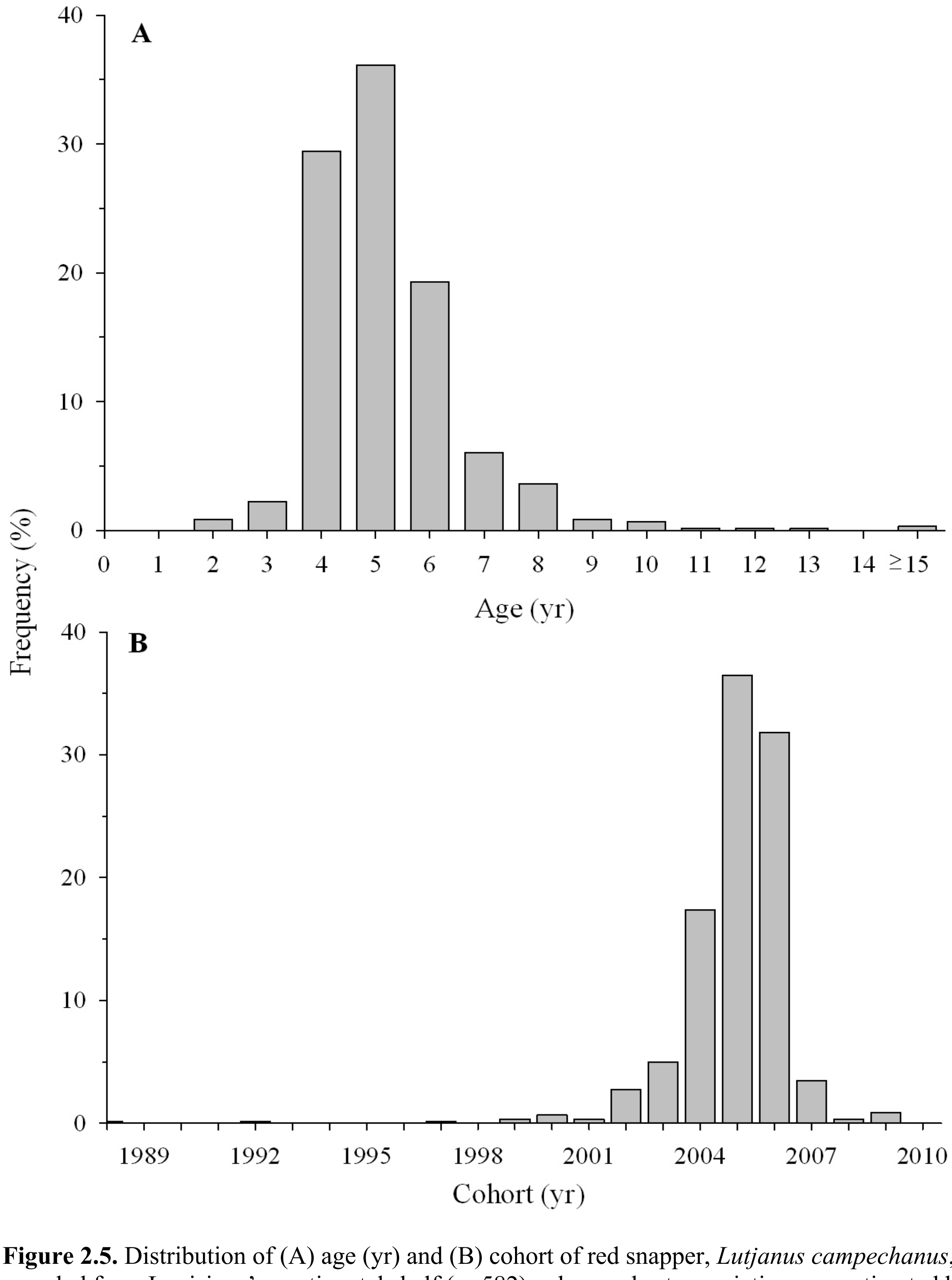

Figure 2.5. Distribution of (A) age (yr) and (B) cohort of red snapper, *Lutjanus campechanus*, sampled from Louisiana's continental shelf (n=582), where cohort association was estimated by back calculating age from Equation (1).

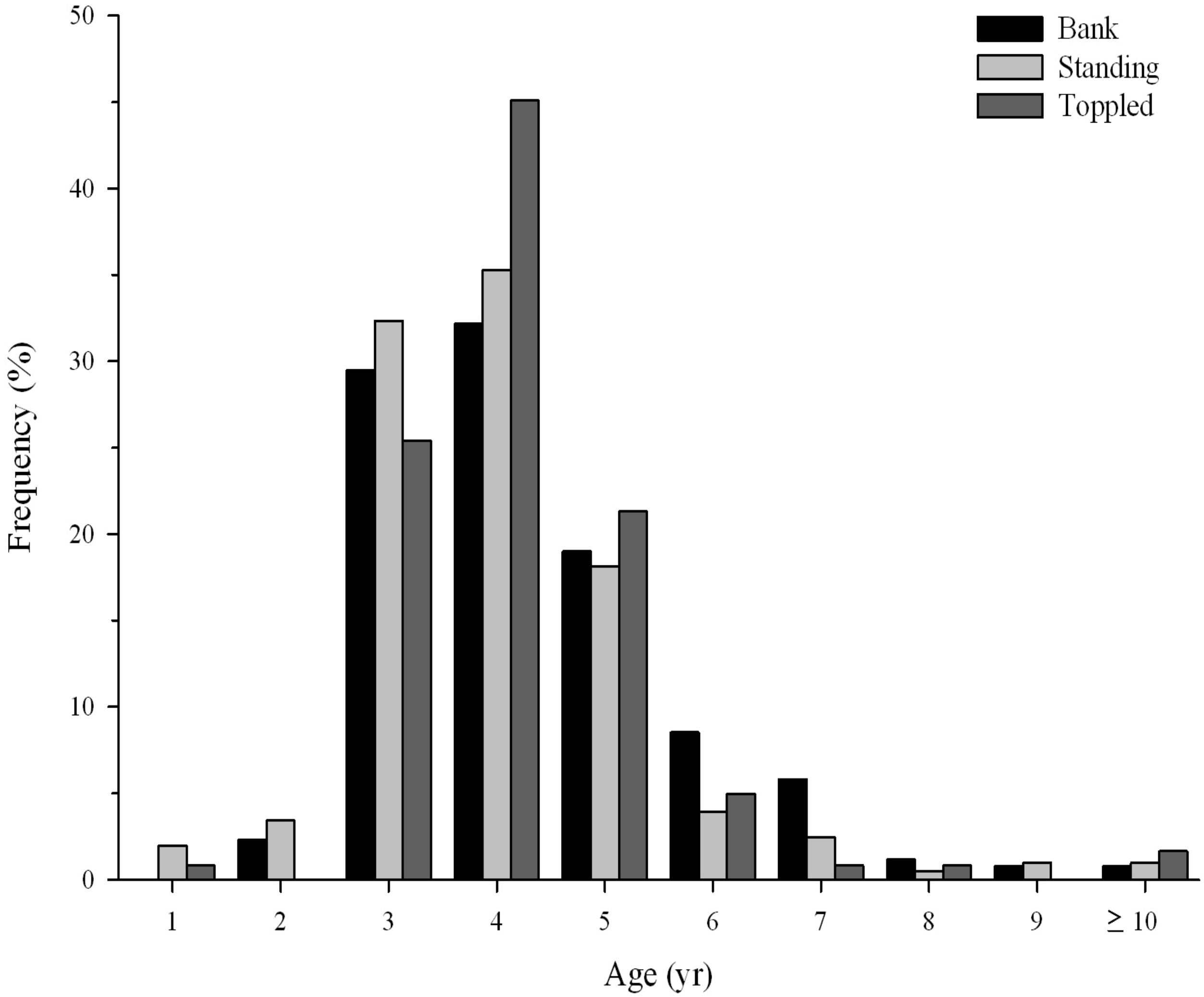

Figure 2.6. Distributions of age in yr for red snapper, *Lutjanus campechanus*, sampled from shelf edge banks (n=256), standing platforms (n=204), and toppled platforms (n=121) on Louisiana's continental shelf.

the banks were significantly older than those from the standing platforms (Tukey's test: p=0.0296), however there was not a significant difference among the age frequency distributions between the two sites (P>KSa: p=0.3038). No significant differences were found between the mean ages and age frequency distributions of red snapper from the banks and toppled platforms (Tukey's test: p=0.7542; P>KSa: p=0.4199). Also, no significant differences in mean age and age frequency were found between the standing and toppled platforms (Tukey's test: p=0.3429; P>KSa: p=0.2634). However, the banks had a slightly larger proportion of red snapper older than 5 yr; 17.1% of the red snapper from the banks were older than 5 yr, compared to 8.8% of the red snapper from the standing platforms and 7.4% from the toppled platforms (Fig 2.6).

2.3.2 Growth

Along with the differences in size and age distributions, there were significant differences among the three habitats in the mean size-at-age of red snapper (Fig 2.7). Mean size-at-age was evaluated only for the most common ages (3-6 yrs) due to insufficient sample size of red snapper from the younger (< 3 yrs) and older (> 6 yrs) age classes. Total length-at-age and total weight-at-age displayed the same significant differences according to the ANOVA and Tukey's Studentized Range (HSD) Test (Tables 2.3 and 2.4), and therefore they will be collectively referred to as size-at-age. Red snapper from the banks were consistently smaller at age than red snapper from the standing and toppled platforms (Fig 2.7). At ages 3, 4 and 5, red snapper from the banks displayed a significantly smaller size-at-age than red snapper from the standing and toppled platforms (Tables 2.3 and 2.4). No consistent pattern in mean size-at-age was observed between red snapper from the standing and toppled platforms (Fig 2.7). Mean size-at-age of red snapper from the standing and toppled platforms were significantly different for ages 3, 4 and 5 but not for age 6 for mean TL at age (Table 2.4), and they were significantly different for ages 3 and 5 but not for ages 4 and 6 for mean TW at age (Table 2.5). No significant difference in mean size-at-age was found among age 6 red snapper from the three habitat types (Tables 2.3 and 2.4). Statistical comparisons of size-at-age for red snapper older than age 6 were not possible due to insufficient sample size.

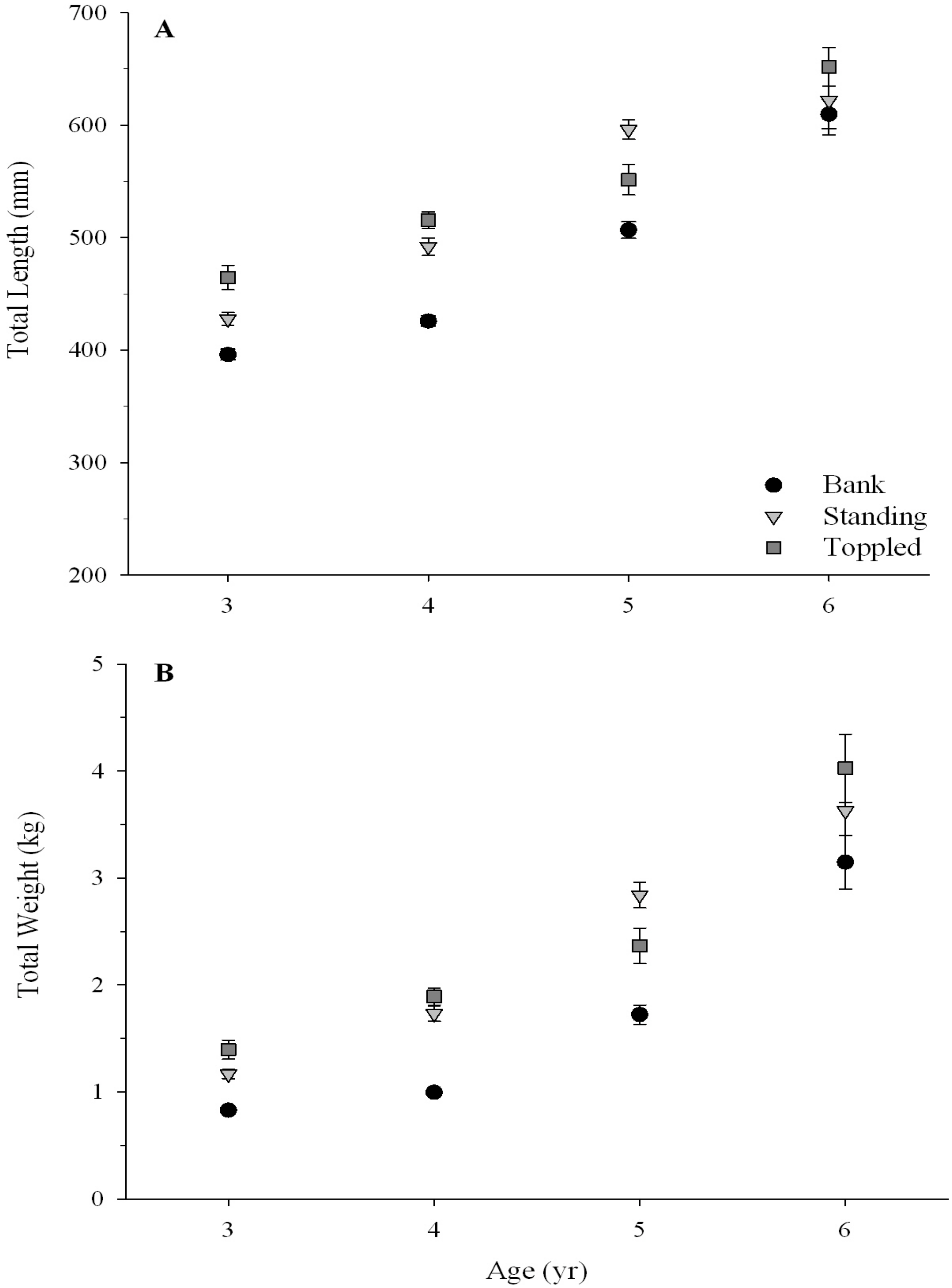

Figure 2.7. Mean (A) total length at age and (B) total weight at age for common ages of red snapper, *Lutjanus campechanus*, by habitat type (i.e. banks, standing platforms, and toppled platforms) on Louisiana's continental shelf. Error bars represent standard error of the mean (SE).

Table 2.4. Analyses of variance and Tukey's Studentized Range (HSD) Tests on red snapper, *Lutjanus campechanus*, mean total length (mm) at age (yr) by habitat type (i.e. banks, standing platforms and toppled platforms on Louisiana's continental shelf) for the most common ages sampled (ages 3-6 yrs). Within each age, similar letters indicate no difference in mean total length ($\alpha = 0.05$).

	ANOVA		Tukey's (HSD) comparison of mean TL at age by habitat		
Age (yr)	F	P	Bank	Standing	Toppled
3	23.96	<0.0001	A	B	C
4	52.28	<0.0001	A	B	C
5	26.39	<0.0001	A	B	C
6	0.99	0.3836	A	A	A

Table 2.5. Analyses of variance and Tukey's Studentized Range (HSD) Tests on red snapper, *Lutjanus campechanus*, mean total weight (kg) at age (yr) by habitat type for the most common ages sampled (ages 3-6 yrs). Within each age, similar letters indicate no difference in mean total weight ($\alpha = 0.05$).

	ANOVA		Tukey's (HSD) comparison of mean TW at age by habitat		
Age (yr)	F	P	Bank	Standing	Toppled
3	34.89	<0.0001	A	B	C
4	65.22	<0.0001	A	B	B
5	26.20	<0.0001	A	B	C
6	1.61	0.2156	A	A	A

Red snapper growth was modeled from observed TL at age and TW at age using the von Bertalanffy growth equation for all ages (Fig 2.8, 2.9 and 2.10). Significant differences in the TL and TW von Bertalanffy growth models were noted among the habitats (TL models likelihood ratio test; χ^2=126.3402; df=4; p=2.36x10^{-26}; TW models likelihood ratio test; χ^2=137.0795; df=4; p=1.19x10^{-28}). However, no significant differences were noted between the von Bertalanffy models for the sexes (TL models likelihood ratio test; χ^2=0.4886; df=2; p=0.7832; TW models likelihood ratio test; χ^2=1.8438; df=2; p=0.3978). Resultant von Bertalanffy growth equations are given in Table 2.6.

Table 2.6. Von Bertalanffy growth models of A. total length at age and B. total weight at age for red snapper, *Lutjanus campechanus*, sampled from banks, standing platforms, and toppled platforms on Louisiana's continental shelf.

A.	**Habitat**	**Von Bertalanffy TL Model**
	Bank	$TL_t=732.6(1-e^{-0.2415(t)})$
	Standing	$TL_t=804.3(1-e^{-0.2505(t)})$
	Toppled	$TL_t=747.0(1-e^{-0.2951(t)})$

B.	**Habitat**	**Von Bertalanffy TW Model**
	Bank	$TW_t=7.3597(1-e^{-0.1972(t)})^{2.96}$
	Standing	$TW_t=7.7054(1-e^{-0.2439(t)})^{2.96}$
	Toppled	$TW_t=8.3857(1-e^{-0.2299(t)})^{2.96}$

Von Bertalanffy models of red snapper TL at age were significantly different among all three habitats (likelihood ratio test; χ^2=236.75; df=2; P=3.89x10^{-52}). The growth model of red snapper from the standing platforms displayed a significantly larger estimate of L_∞ than the estimates from the banks and toppled platforms models (Table 2.7 A and C, Fig 2.10A). The L_∞ estimates did not differ significantly between the models of red snapper from the banks and toppled platforms (Table 2.7B, Fig 2.10A). Significant differential growth in TL was displayed between the model estimates of *k* (Table 2.7 and Fig 2.8). The model of red snapper from the toppled platforms displayed a significantly faster growth coefficient (*k*) than the estimates of *k* in the models of red snapper from the banks and standing platforms (Table 2.7 B and C, respectively). The *k* estimates did not differ significantly between the models of red snapper from the banks and standing platforms (Table 2.7A, Fig 2.10A).

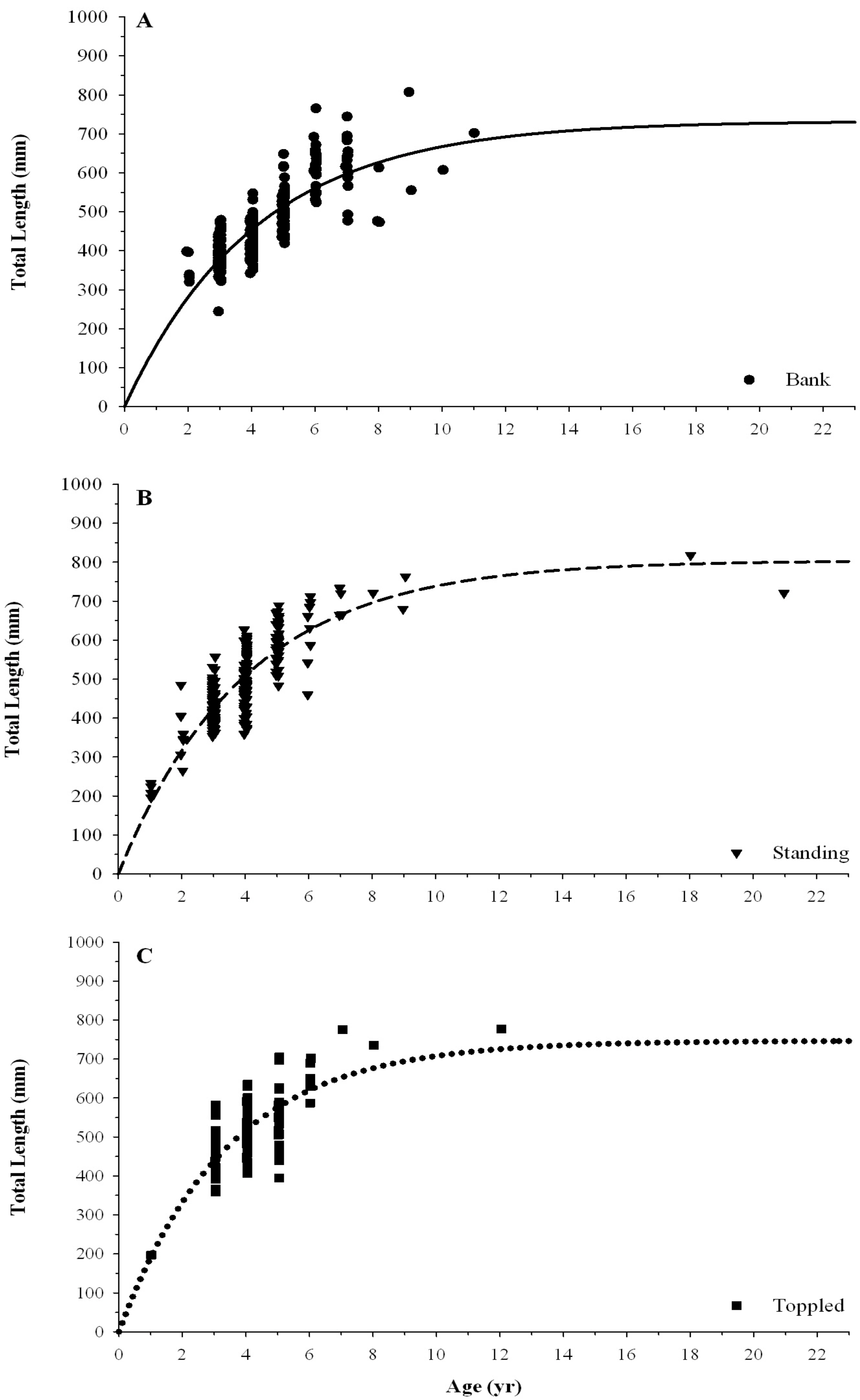

Figure 2.8. Observed total length (mm) at age (yr) for red snapper, *Lutjanus* campechanus, from (A) banks, (B) standing platforms, and (C) toppled platforms on Louisiana's continental shelf. Plotted lines represent the von Bertalanffy growth functions fitted to the data from each habitat.

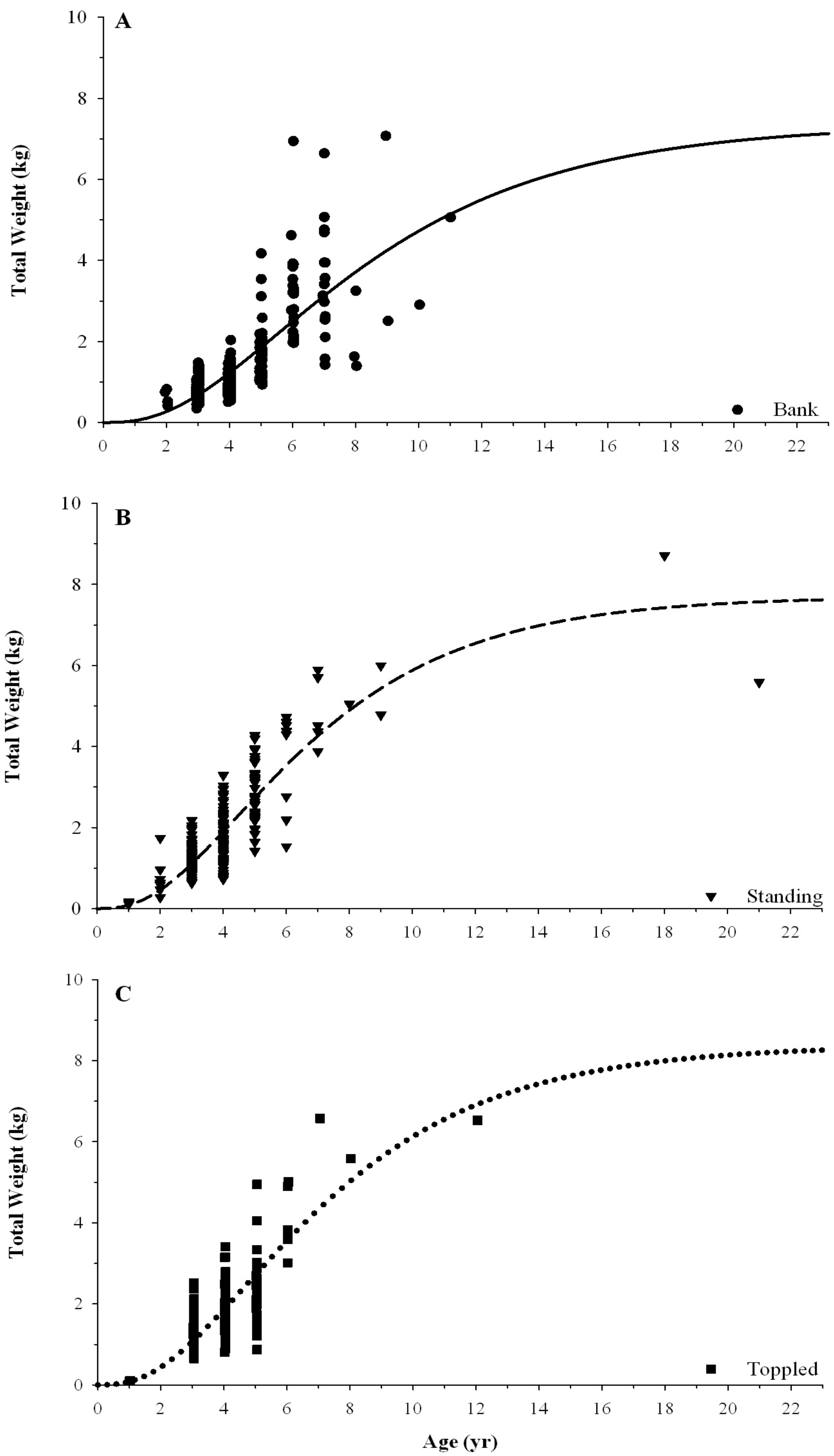

Figure 2.9. Observed total weight (kg) at age (yr) for red snapper, *Lutjanus* campechanus, from (A) banks, (B) standing platforms, and (C) toppled platforms on Louisiana's continental shelf. Plotted lines represent the von Bertalanffy growth functions fitted to the data from each habitat.

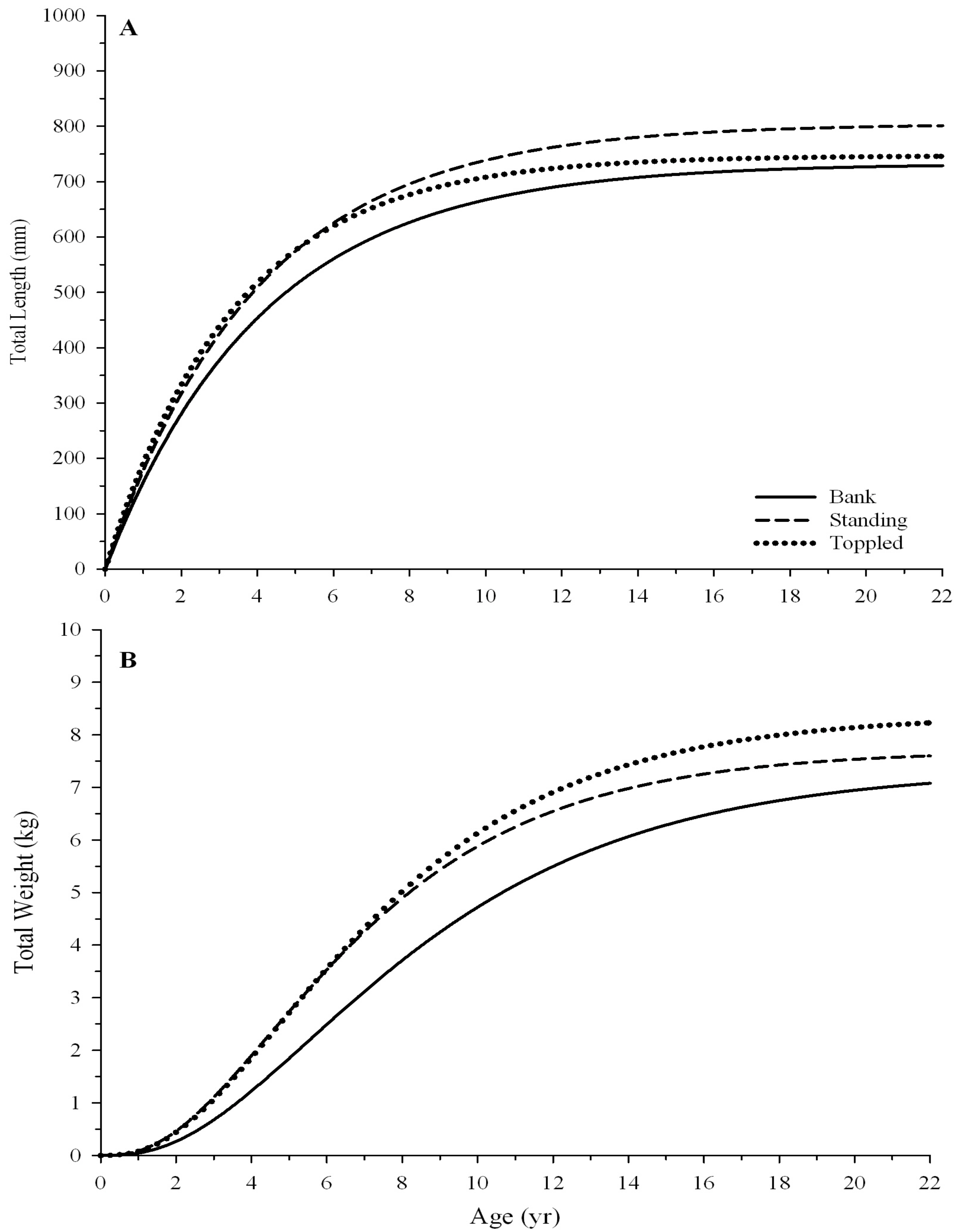

Figure 2.10. Von Bertalanffy growth equations of (A) total length (mm) at age (yr) and (B) total weight (kg) at age (yr) for red snapper, *Lutjanus campechanus*, sampled from banks, standing platforms, and toppled platforms on Louisiana's continental shelf.

Table 2.7. Chi-square (χ^2), degrees of freedom (df), and P-values for likelihood ratio tests for comparing red snapper, *Lutjanus campechanus*, TL von Bertalanffy growth models and parameters among A) banks and standing platforms B) shelf-edge banks and toppled platforms and C) standing and toppled platforms on Louisiana's continental shelf.

A	**Bank vs Standing**		
	TL model	**L_∞**	**k**
χ^2	140.39	11.16	0.01
df	2	1	1
P	3.274×10^{-31}	0.0008	0.9116
B	**Bank vs Toppled**		
	TL model	**L_∞**	**k**
χ^2	102.76	1.22	4.07
df	2	1	1
P	4.86×10^{-23}	0.2686	0.0437
C	**Standing vs Toppled**		
	TL model	**L_∞**	**k**
χ^2	8.17	51.31	6.27
df	2	1	1
P	0.0168	7.89×10^{-13}	0.0126

Table 2.8. Chi-square (χ^2), degrees of freedom (df), and P-values for likelihood ratio tests for comparing red snapper, *Lutjanus campechanus*, TW von Bertalanffy growth models and parameters among A) banks and standing platforms B) banks and toppled platforms and C) standing and toppled platforms on Louisiana's continental shelf.

A	**Bank vs Standing**		
	TW model	**W_∞**	**k**
χ^2	177.05	0.64	33.48
df	2	1	1
P	1.95×10^{-38}	0.4237	7.19×10^{-09}
B	**Bank vs Toppled**		
	TW model	**W_∞**	**k**
χ^2	249.26	0.88	4.74
df	2	1	1
P	8.63×10^{-24}	0.3492	0.0295
C	**Standing vs Toppled**		
	TW model	**W_∞**	**k**
χ^2	1.75	1.70	1.67
df	2	1	1
P	0.4161	0.1922	0.1959

Von Bertalanffy models of red snapper TW at age were also significantly different among the habitats (likelihood ratio test; χ^2=412.75; df=2; P=1.52x10^{-54}). While the models were significantly different from each other, no significant were noted among the estimates of W_∞ (Table 2.8 A, B and C, Fig 2.10B). Significant differential growth in TW was displayed between the model estimates of *k* (Table 2.8 and Fig 2.9). The models from the standing and toppled platforms displayed significantly larger estimates of *k* than the model of red snapper from the banks (Table 2.8 A and B). No significant differences in the *k* estimates were noted between the models of red snapper from the standing and toppled platforms (Table 2.8 C and Fig 2.10B).

All red snapper exhibited rapid growth until approximately age 6 to 8, after which growth slowed considerably (Fig 2.8 and Fig 2.9). Therefore, red snapper growth was modeled from observed TL and TW at age using linear regressions to assess rapid growth for red snapper aged 1 to 7 yr (Fig 2.11, A and B). The linear regressions of TL at age for red snapper are given in Table 2.9.

Table 2.9. Linear regression models of TL at age for red snapper, *Lutjanus campechanus*, sampled from banks, standing platforms, and toppled platforms on Louisiana's continental shelf.

Site	Regression Model	df	F	p-value	r^2
Banks	TL = 61.74Age + 199.33	247	527.63	<0.0001	0.681
Standing	TL = 75.82Age + 195.81	197	400.63	<0.0001	0.670
Toppled	TL = 59.77Age + 273.79	117	92.00	<0.0001	0.440

The linear regressions of weighted mean TL at age for red snapper aged 1 to 7 yr were significantly different among all three habitats (Fig 2.11A) (ANCOVA test for homogeneity of slopes, $F_{2,561}$=5.32; p=0.0051; ANCOVA test for equal intercepts, $F_{2,561}$=4.44; p=0.0122). The red snapper from the standing platforms exhibited the smallest intercept and those from the toppled platforms exhibited the largest. The regression of red snapper from the standing platforms exhibited a significantly larger slope than the regression of red snapper from the banks and toppled platforms (ANCOVA test for homogeneity of slopes, $F_{1,444}$=9.61; p=0.0021; and ANCOVA test for homogeneity of slopes, $F_{1,314}$=4.99; p=0.0262). No significant difference was detected between slopes of the regressions from the banks and toppled platforms (ANCOVA test for homogeneity of slopes, $F_{1,364}$=0.10; p=0.7524), however a significant difference was noted between the intercepts (ANCOVA test for equal intercepts, $F_{1,364}$=8.07; p=0.0.0048). A significant difference in intercepts was also detected between red snapper from the standing and toppled platforms (ANCOVA test for equal intercepts, $F_{1,314}$=6.91; p=0.0090).

Observed TW at age was also examined among habitats for red snapper 1 to 7 yr in age as described above (Fig 2.11B). Resultant linear growth regressions for TW at age are given in Table 2.10.

Table 2.10. Linear regression models of TW at age for red snapper, *Lutjanus campechanus*, sampled from banks, standing platforms, and toppled platforms on Louisiana's continental shelf.

Site	Regression Model	df	F	p-value	r^2
Banks	TW = 0.659Age – 1.356	247	358.43	<0.0001	0.592
Standing	TW = 0.791Age – 1.231	197	381.28	<0.0001	0.659
Toppled	TW = 0.716Age – 0.901	117	105.32	<0.0001	0.474

Significant differences in slopes were detected when comparing red snapper from the three habitats (ANCOVA test for homogeneity of slopes, $F_{2,561}$=2.95; p=0.0532). The regression of red snapper from the standing platforms exhibited a significantly larger slope than the regression of red snapper from the banks (ANCOVA test for homogeneity of slopes, $F_{1,444}$=6.05; p=0.0141). No significant difference was noted between the slopes of the regressions of red snapper from the toppled platforms and banks (ANCOVA test for homogeneity of slopes, $F_{1,364}$=0.89; p=0.3451). No significant differences were found between the slopes of the

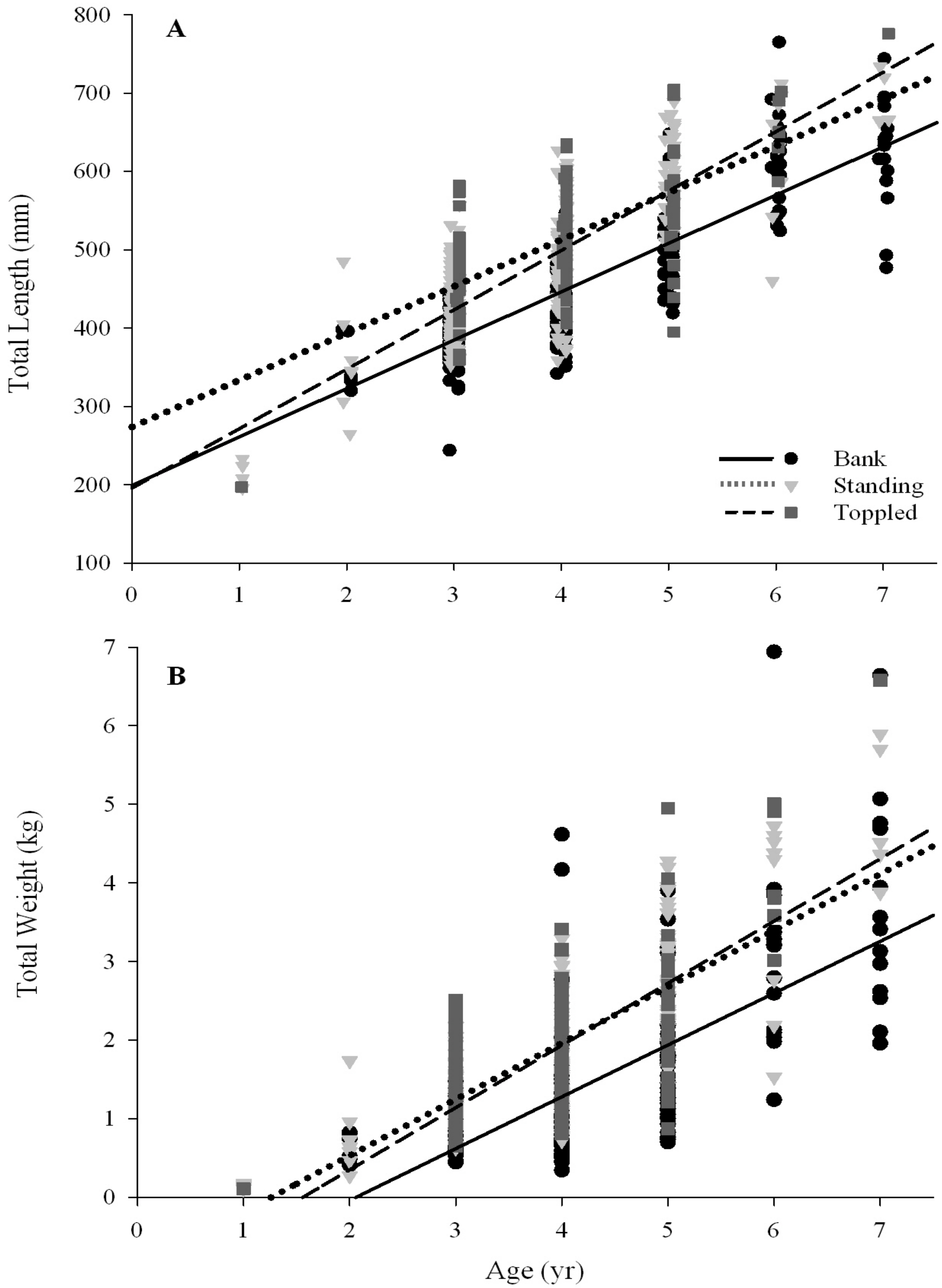

Figure 2.11. Linear regression of observed (A) total length (mm) at age (yr) and (B) total weight (kg) at age (yr) of red snapper, *Lutjanus campechanus*, aged 1 to 7 yr from shelf edge banks, standing platforms, and toppled platforms on Louisiana's continental shelf.

regressions of red snapper from the standing and toppled platforms (ANCOVA test for homogeneity of slopes, $F_{1,314}$=0.57; p=0.4508). No significant differences were detected among the intercepts of all three habitat models (ANCOVA test for equal intercepts, $F_{2,561}$=0.74; p=0.4785).

2.4 Discussion

2.4.1 Age Structure

Overall, red snapper exhibited a truncated age structure. Smaller sizes and younger ages of red snapper were observed in this study compared to previous reports (Patterson et al. 2001; Wilson and Nieland 2001; Fischer et al. 2004). The dominant age classes represent the strong 2004, 2005 and 2006 year classes (SEDAR 2009; Cowan 2011). Like many commercial fishes, red snapper exhibit a periodic life history strategy distinguished by delayed maturation (red snapper do not reach maximum spawning potential until 12-15 yr of age (Render 1995; Woods et al. 2003)), longevity, high fecundity, synchronous spawning, and small egg size (Winemiller and Rose 1992; Winemiller and Rose 1993; Cowan et al. 2010). Their bet-hedging reproductive strategy and protracted spawning seasons are reported to produce a strong year class every 5-10 yr (Allman and Fitzhugh 2007). When combined with their longevity, this periodic occurrence of strong year classes is sufficient to maintain a stable population biomass under modest harvesting (Cowan et al. 2010). However, when under prolonged overfishing, periodic strategists will take a much longer time to recover due to the infrequency of strong year classes (Winemiller and Rose 1992; Secor 2000; Cowan et al. 2010). Thus, identification and protection of the strong year classes are requisite to allow the stock to recover. Protection of the strong year classes will allow more fish to reach maximum spawning potential, which is crucial for stock recovery given that reproductive success (increased fecundity and larval survivorship) increases with maternal age (Berkeley et al. 2004; Palumbi 2004; Walsh et al. 2006).

The oldest red snapper from this study was 21 yr old, which is less than half of the age the oldest reported red snapper in the GOM (57 yr) (Allman and Fitzhugh 2007). The absence of truly old red snapper in this study may be a result of the intense overfishing that occurred during the mid to late 1900s, which brought the GOM red snapper stock to its most depleted state about 20 yr ago (late 1980s early 1990s) (SEDAR 2009; Cowan et al. 2010). This large decrease in the spawning stock biomass resulted in weak year classes, producing only two dominant year classes between 1980 and 2000 (Allman and Fitzhugh 2007; SEDAR 2009), and is a plausible reason why there is a scarcity of older fish (>15 yr) observed today (Allman and Fitzhugh 2007; Nieland et al. 2007; SEDAR 2009). Samples from this study indicate that relatively few members of these strong year classes (n=1 for the 1980 year class and n=0 for the 1995 year class) may have survived to ages of maximum spawning potential (12-15 yr).

Other possible reasons for the absence of old red snapper in this study are sample size and discrete sampling stations with limited spatial coverage. The sample size in this study (n=582) is small compared to previous red snapper age and growth studies (n=5192 Fischer et al 2004 and n=3791 Wilson and Nieland 2001). Thompson (1987) showed that a sample size of about 510 is sufficient to capture all age-class proportions, however, there are several potential biases that are inherent in this study. Specifically, this study sampled red snapper from a limited number of stations (Banks n=4, Standing Platforms n=3, Toppled Platforms n=2) on Louisiana's continental shelf. Also due to sampling logistics, these stations were relatively close to each other (several stations were within 10 km of each other, and the farthest distance between stations was approximately 100 km, Figure 2.1). Therefore, it must be taken into consideration that these results may not be representative of the entire population of red snapper on the Louisiana shelf.

While the oldest red snapper in this study was collected from a standing platform, the standing platforms do not appear to support many old red snapper (4.3% were >6 yr). The highest proportion of relatively old (>6 yr) red snapper was 8.5% on the banks. Red snapper exhibit an ontogenetic habitat preference, typically moving from low relief shell rubble and reef habitats as juveniles to higher relief hard substrate in deeper water as young adults, with adults of ages 2 to ~9 yr showing a strong affinity for structure, inhabiting both natural hard-bottom and artificial habitats (Nelson and Manooch 1982; Workman and Foster 1994; Nieland and Wilson 2003; Geary et al. 2007; Wells and Cowan 2007(Gledhill 2001)). It has also been hypothesized that in the northwestern GOM, red snapper emigrate away from the oil and gas platforms and high relief structures to natural hard-bottom habitats further offshore as they age past ~9 yr (Dennis and Bright 1988; Gledhill 2001; Nieland and Wilson 2003; Mitchell et al. 2004; Geary et al. 2007; Wells and Cowan 2007; Gallaway et al. 2009). For example, Nieland and Wilson (2003) documented a drastic decrease in red snapper older than 3 yr of age around an oil and gas platform off Louisiana's coast and several fishery-dependent and fishery-independent surveys have collected older, larger red snapper (up to 53 yr; median age 12, median TL 784 mm) along the shelf edge in the western GOM (Mitchell et al. 2004; Allman and Fitzhugh 2007; SEDAR 2009). This current study supports the theory that red snapper move further offshore as they age, however, the word 'old' is used here in relative terms because extremely low numbers of red snapper older than 10 yr were found in this study (<0.5%). This study is also consistent with the recent NMFS report that a large, offshore or deepwater cryptic biomass of red snapper does not exist in the northern GOM (SEDAR 2009).

2.4.2 Growth Models

The von Bertalanffy growth models of total length at age estimated in this study indicate significant differences in the growth of red snapper among the habitats sampled, with a slower growth coefficient and smaller maximum theoretical total length exhibited by red snapper from the natural shelf-edge banks. However, these differences need to be viewed with caution because very few red snapper older than 10 yr were collected in this study and large variability in size at age was observed, making it difficult to compare growth rates. For instance, the lack of older fish could result in biased asymptotes. Normally, a lack of older fish drives the L_∞ estimate higher than expected and does not allow the curve to flatten, as seen in the large L_∞ (1025 mm TL) reported by Szedlmayer and Shipp (1994). However, the sample size of red snapper older than 10 yr in this study did not produce abnormally large estimates of L_∞. The ability of the models to reach asymptotes may be the result of the models being forced through $t_0=0$. Forcing the models through $t_0=0$ allowed for comparison of growth characteristics after individuals settled on the habitats sampled, and was performed under the assumption that the growth differences occurred after the fish settled on the various habitats.

The difference in L_∞ estimates seen in this study may be attributable to the influence of the two red snapper older than 12 yr from the standing platforms and the lack of older red snapper from the toppled platforms and banks. None of the red snapper collected from the toppled platforms were older than 12 yr (Fig 2.8C), however, the curve was still able to 'heal-over' and reach an asymptote most likely resulting from the forcing of the model through $t_0=0$. The L_∞ estimate for red snapper from the toppled platforms may have been heavily influenced by the consistency in size at age among the three relatively old red snapper from this habitat (Fig 2.8C), while the low L_∞ estimate for red snapper from the banks appears to be strongly influenced by the large variability in TL at ages 6 to 10 yr (Fig 2.8 A). Also, red snapper growth appears to be leveling off around the ages of 6 to 8 yr old, causing the von Bertalanffy growth models to predict lower L_∞ estimates (Fig 2.8).

The von Bertalanffy growth models of total weight at age from this study support the total length at age models. These models indicate that red snapper from the shelf-edge banks grow at a significantly slower rate than red snapper from the standing and toppled platforms. Unlike the TL von Bertalanffy models, the TW models suggest that red snapper from the toppled platforms exhibit faster growth than the red snapper from the other two habitats. However the estimates of k and W_∞ can be greatly influenced by the size of the older fish, forcing the curve to 'heal-over' at younger ages if there is high variability in the size at age, as seen in the banks model (Fig 2.9 A), or resulting in the inability of the curve to 'heal-over' if there is a lack of older fish, as seen in the toppled platforms model (Fig 2.9 C). The relatively low estimate of W_∞ for the standing platforms model is most likely due to the influence of the small weight of oldest red snapper on that habitat (Fig 2.9 B).

The mean size-at-age data from this study support the growth rate differences estimated with the von Bertalanffy models. Red snapper from the shelf-edge banks were consistently smaller at age than red snapper from the standing and toppled platforms for ages 3-5 yr. The lack of a significant difference in size-at-age-6 red snapper among the habitats is most likely due to high variance in the size measurements at age 6 (Fig 2.7 A and B). However, size-at-age of red snapper from the shelf-edge banks did not continue to increase after age 6 as it did for red snapper from the standing and toppled platforms (Fig 2.8 A and Fig 2.9 A). Thus suggesting that red snapper from the shelf-edge banks grow slower and reach smaller maximum sizes than red snapper from the standing and toppled platforms.

The von Bertalanffy growth models in the present study were similar to previous reports of red snapper growth models. The total length at age models predicted similar values of L_∞ and *k* to those reported in previous studies (Szedlmayer and Shipp 1994; Render 1995; Patterson et al. 2001; Wilson and Nieland 2001; Fischer et al. 2004). The L_∞ estimates for all three models were smaller than red snapper age and growth studies from the 1990s (Szedlmayer and Shipp 1994; Patterson et al. 2001; Wilson and Nieland 2001). These smaller L_∞ estimates coincide with the recent decline in size of red snapper (Nieland et al. 2007) and are similar to the more recent estimates of L_∞ for red snapper from the northern Gulf of Mexico (778.2-847.8 mm FL) reported by Fischer et al. (2004).

Von Bertalanffy models from this study predicted *k* values that are faster than the earlier age and growth studies of red snapper, including Szedlmayer and Shipp (1994), Patterson et al. (2001) and Wilson and Nieland (2001), which ranged from 0.15 to 0.194. This study's *k* estimates were more similar to the faster *k* estimates reported by Fischer et al. (2004) (0.25 – 0.38). These faster growth estimates may be a compensatory response to overexploitation (Trippel 1995; Berkeley et al. 2004; Nieland et al. 2007) or they may correspond to the increased productivity from the Mississippi River plume (Grimes 2001; Fischer et al. 2004). Previous studies have suggested that the nutrient-rich waters of the Mississippi River plume enhance productivity on Louisiana's continental shelf and may be more conducive to faster growth for numerous fish species including red snapper (DeVries et al. 1990; Fischer et al. 2004). However, very few red snapper under the age of 3 yr were collected in this study and therefore the von Bertalanffy growth models were forced through $t_0=0$ in order to more accurately predict juvenile growth. Forcing t_0 through zero may increase estimates of *k,* which could explain the similarity between this study's *k* estimates and those reported by Fischer et al. (2004) who also forced their von Bertalanffy models through t_0=0.

While the von Bertalanffy growth models of total weight at age from this study were similar to previous estimates, it appears that red snapper from all three habitats reach a smaller maximum total weight than red snapper from previous studies in the northwestern GOM (Render 1995; Fischer et al. 2004). The largest value of W_∞ estimated in this study was at the lower end of the W_∞ estimates reported previously (Render 1995; Fischer et al. 2004). However, this W_∞ value was estimated from the sample of young red snapper at the toppled platforms, which only contained three individuals older than 6 yr. Also, estimates of the length-weight coefficient *b* (Combined: b=2.86, Standing platforms: b=2.84, Toppled Platforms: b=2.92, Banks: b=3.02) were at the smaller end of previously reported values, which range from 2.84 to 3.17 with a mean of 3.00 (Nelson and Manooch 1982; Render 1995; Patterson et al. 2001; Wilson and Nieland 2001; Fischer et al. 2004), which is expected for fish with isometric growth (Anderson and Neumann 1996). This study's estimates of *b* suggest that red snapper might not be growing as isometric as previous estimates.

The von Bertalanffy models from this study also indicated rapid linear growth during the first several years of age. Szedlmayer and Shipp (1994) and Fischer et al. (Fischer et al. 2004) both documented rapid linear growth of red snapper up until age 10. In this study, the red snapper also exhibited a period of rapid, linear growth, however, the von Bertalanffy growth models showed that red snapper from all habitats exhibit rapid growth until approximately 6 or 7 yr of age, not 10 yr. Therefore linear regressions of total length and total weight at age were modeled for ages 1-7. Regressions of total length and total weight at age indicated significantly slower rates for red snapper from the shelf-edge banks and toppled platforms than from the standing platforms. The red snapper from the shelf-edge banks exhibited rapid linear growth until age 5 or 6, and is noted in the lack of significance between the regression rates of red snapper aged 1-7 from the shelf-edge banks and the toppled platforms (both total length and total weight at age). This difference in linear growth rate is due to the slowing of somatic growth of red snapper from the shelf-edge banks earlier in life than the red snapper from the standing platforms. It appears that red snapper are devoting more of their energy as younger fish to reproductive rather than somatic growth. For instance, an ongoing study of red snapper reproductive biology indicates that red snapper from the shelf-edge banks and toppled platforms are maturing faster than red snapper from standing platforms (Kulaw, personal communication[1]).

2.4.3 Possible Causes for Habitat-Specific Differences

The habitat-specific differences noted in this study may be driven by numerous environmental and anthropogenic factors. The predominance of small, young red snapper in this study reflects the recent decline in size at age of red snapper (Nieland et al. 2007) as well as the age truncation of the population (Allman et al. 2009) due to overfishing (Berkeley et al. 2004). Several compensatory responses to fishing pressure, including age truncation, faster growth and early maturation, have been noted in the GOM red snapper stock (Fischer et al. 2004; Jackson et al. 2007; Nieland et al. 2007; Allman et al. 2009) and are present in this study. These compensatory responses are classic signs of overexploitation and juvenescence (Trippel 1995; Nieland et al. 2007). Removal of the largest, and oldest fish results in a truncated age distribution and can have substantial negative effects on the population's recovery (Leaman and Beamish 1984; Trippel et al. 1997). Because fecundity increases with fish size and age and longevity

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[1] Kulaw, D.K. 2011. Louisiana State University. Department of Oceanography and Coastal Sciences.

extends reproduction across a long period of time, truncating the age distribution of the stock decreases its reproductive capabilities and could impose severe limitations on population recovery (Leaman and Beamish 1984; Trippel et al. 1997; Berkeley et al. 2004; Palumbi 2004). Other documented maladaptive responses to fishing pressure include earlier maturation (juvenescence), smaller egg volume, lower larval survival, and lower fecundity (Trippel 1995; Walsh et al. 2006). All of which greatly reduce the population's capacity for recovery.

Another life history response to fishing pressure that can be manifested in a population is the predominance of slower growth rates. Fishing pressure has been shown to affect daily growth rates of juvenile (age-0) red snapper in the north-central GOM, with slower growth observed on trawled habitats and faster growth on untrawled habitats (Wells et al. 2008). The selective removal of rapidly growing fish inadvertently selects for the survival of slow-growing individuals, in turn changing the biological reference points and altering the life history strategy of the population (Trippel et al. 1997; Zhao et al. 1997; Walsh et al. 2006; Nieland et al. 2007). Typically, red snapper recreational fishermen target the largest fish and commercial fishermen target fish close to minimum size, both selecting for the fastest growing fish. Since the implementation of the IFQ system, commercial fishermen are not constrained a set season and they have the capability to travel further offshore and for longer periods of time. This gives them the potential to focus more of their fishing effort on the shelf-edge habitats. Thus, the differing growth rates found in this study may suggest that the natural shelf-edge banks are experiencing higher levels of harvest pressure. Also, previous studies have shown that fast-growing two and three year old red snapper recruit to oil and gas platforms, and there appears to be a drastic decrease in the number of fish older than three yr around these platforms (Nieland and Wilson 2003). The combination of increased commercial fishing pressure along with the emigration of older red snapper away from oil and gas platforms may explain the dominance of slow-growing individuals on the shelf-edge banks.

The habitat-specific differences in red snapper age and growth parameters may also be due to structural and environmental differences among the habitats as well as age-specific preferences. The three habitats differ significantly in structure, which influences the available refuge habitat, foraging opportunities, and community dynamics (Pickering and Whitmarsh 1997). These three habitats represent a gradient of relief in the water column: the vertical relief of the standing platforms spans the entire height of the water column, connecting the benthos to the photic zone, and the toppled platforms also take up a substantial portion of the water column, however they are cut off around 25 m below the surface, while the shelf-edge banks provide natural high relief from the deep (>100m) continental slope, but do not extend shallower than 50 - 60 m from the surface. Both the standing and toppled platforms contain numerous pipe systems and columns that create a substantially different habitat than that provided by the shelf-edge banks' rocky outcrops.

All of these habitats are also influenced by the hydrodynamic patterns of the surrounding ecosystem. Strong currents have been noted on the outer continental shelf and both platform types may serve as refuge to fish by diverting the strong shelf-edge currents (Pickering and Whitmarsh 1997). Another environmental condition that may be influencing the growth of red snapper across all of these habitats is the proximity of these habitats to the mouth of the Mississippi River. The river plume inputs high nutrient levels and increased levels of sediments onto Louisiana's continental shelf. The increased sedimentation rates on these habitats may influence the suitability of the reef habitats, and one hypothesis is that the smaller estimates of L_∞ and W_∞ may be correlated with increased sedimentation rates. It would be beneficial for future research to examine red snapper age and growth parameters across the shelf edge banks in the northwestern GOM from the mouth of the Mississippi River to the western banks off Texas, such at the Flower Garden Banks.

Red snapper growth may also be influenced by the quantity and quality of the prey available on the different habitats. The faster growth rate exhibited by the red snapper from the standing platforms may be correlated with increased food availability and benthic primary productivity resulting from the connectivity to the productive photic zone provided by the standing platforms' vertical habitat (Stanley and Wilson 1996; Wilson et al. 2003; Daigle 2011). While recent red snapper gut content investigations indicate differences in prey types among the habitats, nutritional value of prey associated with each habitat is not correlated with red snapper growth and there is no indication of more nutritious diets near standing platforms (Simonsen, personal communication[2]). The trophic pathways and food web bases also differ between the habitats. Daigle (2011) found two trophic pathways exist around platforms in the GOM, one driven solely by phytoplankton (toppled platforms) and one by both benthic algae and phytoplankton (standing platforms). Wilson et al. (2003) also found significant differences in fish biomass and community structure among standing, toppled and partially removed platforms, as well as natural hard-bottom habitats in the northwestern GOM. Thus, community structure (predator-prey biomass) and the availability of food and refuge may drive the growth differences in the localized red snapper populations around the specific habitats. While no other studies have compared habitat-specific growth parameters for adult red snapper, habitat-specific differences in the daily growth rates of age-0 red snapper have been reported and these differences were

[2] Simonsen, K. A. 2011. Louisiana State University. Department of Oceanography and Coastal Sciences.

attributed to habitat complexity, prey composition, and predator biomass (Wells et al. 2008). Individual habitat preference and age-specific habitat preference may also play a role in the habitat-specific differences observed in this study.

2.5 Conclusions

This study documented habitat-specific differences in red snapper size and age and growth parameters that reflect the phenotypic plasticity found in the GOM red snapper stock, which can be intensified by varying exploitation rates, diet composition, energy allocation, and habitat preference. It is important to note that red snapper from the natural habitats (shelf-edge banks) exhibit a slower growth rate and smaller maximum size than red snapper from artificial habitats (standing and toppled platforms) as well as from previous reports. Also, the natural habitats appear to support a higher predominance of relatively older (>6 yr) red snapper compared to the artificial habitats. However, growth rates were difficult to compare due to a lack of older fish as well as large variability in the size at age data. In order to prevent habitat-specific overfishing and promote stock recovery, the implications of these differences should be considered in future stock assessments and management. Furthermore, these habitat-specific differences should also be weighed when evaluating and delineating essential fish habitat in the northern GOM.

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CHAPTER 3: REGIONAL DIFFERENCES IN RED SNAPPER (*LUTJANUS CAMPECHANUS*) AGE AND GROWTH ACROSS THE GULF OF MEXICO

3.1 Introduction

The Gulf of Mexico (GOM) red snapper (*Lutjanus campechanus*) stock has been exploited since the mid 1800s and is still one of the most economically important fisheries in the GOM. This fishery has multi-million dollar commercial and recreational sectors, and is impacted by bycatch from the shrimp fishery. Since the early 1990s, GOM red snapper have been intensely managed as one unit stock by the Gulf of Mexico Fisheries Management Council (GMFMC) under the Magnuson-Stevens Fishery Conservation and Management Act (MSFCA). However, the GOM red snapper stock has been declining since the 1970s and is currently overfished (Goodyear 1995; SEDAR 2005; GMFMC 2007; Porch 2007). Results of the 2009 stock assessment update indicate that although the GOM red snapper stock is overfished, it is perhaps no longer undergoing overfishing in the western GOM, and the current management policy has set a red snapper rebuilding plan for stock recovery by 2032 (SEDAR 2009; GMFMC 2010).

Even though red snapper in the GOM are currently managed as one unit stock, separate stock assessments have been conducted for sub-units east and west of the Mississippi River since 2004 (SEDAR 2005). Management under the unit stock hypothesis assumes no significant differences in red snapper population structure (genetics and life history characteristics) across the GOM. The unit stock assumption has been supported by early genetic analysis (Camper et al. 1993; Gold et al. 1997; Gold et al. 2001) as well as the capacity of red snapper to move great distances (Patterson et al. 2001). Also, in the past twenty years, two strong year classes (1989 and 1995) were found to dominate gulf-wide (Allman and Fitzhugh 2007), thus strengthening the unit-stock hypothesis. However, in the past decade, numerous studies have highlighted spatial differences in red snapper age, growth and reproductive demographics in eastern versus western GOM red snapper (Allman et al. 2002; Fischer 2002; Fischer et al. 2004; Jackson et al. 2007) as well as differences in red snapper maturation schedules across the GOM (Woods et al. 2003; Jackson et al. 2007). Recent population structure studies of red snapper genetics and movement suggest that GOM red snapper form a metapopulation of semi-isolated, distinct sub-populations (Saillant and Gold 2006; Gold and Saillant 2007; Patterson 2007). Examination of red snapper otolith microchemistry has also shown region-specific natural tags or 'elemental signatures,' which are being used to identify nursery sources, subpopulations, and stock mixing across the GOM (Patterson et al. 2008; Nowling et al. 2011; Sluis, personal communication[1]).

Other considerations for GOM red snapper management and stock assessments include habitat and fishing pressure differences across the regions. Fishing pressure varies significantly across the GOM, with the commercial red snapper fishery and bycatch from the shrimp fishery constituting the main sources of fishing mortality in the western GOM, and the recreational fishery accounting for the greatest source of fishing mortality in the eastern GOM (GMFMC 2007). Habitat complexity and patchiness varies greatly throughout the GOM from soft bottom (mud/sand/silt) to natural hard bottom (shell rubble, rocky outcrops, reefs), and artificial hard substrate (oil platforms, ship wrecks, constructed reefs). The continental shelf across the GOM is predominantly soft bottom, with a scattering of low-relief hard bottom and shelf-edge banks. It has been estimated that natural hard bottom habitat covers 1-3% of the northern GOM shelf, totaling about 2,800 km^2 (Parker et al. 1983), and covering up to 15% in some areas (Schroeder et al. 1995; Dufrene 2005). However, since the boom of oil exploration in the late 1940s, the

[1] Sluis, M. Z. 2011. Louisiana State University, Department of Oceanography and Coastal Sciences.

northern GOM now has an additional 12 km^2 of hard artificial structure in the northwestern GOM (Stanley and Wilson 1997; Gallaway et al. 1998). The productive, nutrient-rich waters of the Mississippi River plume have also been shown to influence fishery production through increased growth rates when compared to other regions of the GOM (DeVries et al. 1990; Grimes 2001).

The objective of this study was to examine the size structure, growth rates, and size-at-age of red snapper across the GOM to elucidate trends in demographic differences noted in the most recent red snapper stock assessments between red snapper east and west of the Mississippi River (SEDAR 2005; SEDAR 2009) as well as reported by Fischer et al (2004) among Texas, Louisiana and Alabama red snapper, and expand the comparison to incorporate the Florida red snapper. This study is timely now because Fischer et al. (2004) made similar measures 10 years ago. Comparison of the demographics and growth parameters from this study should help elucidate changes and trends in region-specific age and growth information for red snapper, and can be used to further evaluate the need for management sub-units.

3.2 Methods

Red snapper were sampled from recreational hook and line fisheries (head boats and charter boats) across the U.S. Gulf of Mexico during the summers of 2009 and 2010 (Figure 3.1). During 2009, red snapper were sampled from recreational fisheries in Clearwater, Florida, Destin, Florida, Dauphin Island, Alabama, Port Fourchon, Louisiana, and South Padre Island, Texas. During 2010, red snapper were not sampled from recreational fishermen in Alabama and Louisiana because of the fishery closure as a result of the Deepwater Horizon Oil Spill. However, red snapper were collected with hook and line from two oil platforms in the Eugene Island block offshore of Louisiana during July 2010. Red snapper were also sampled from recreational fishermen in Galveston, Texas in June 2010. For all fish collected, morphometric measurements were recorded (total length [TL] in millimeters and total weight [TW] in grams when possible), sex was determined by macroscopic examination of gonads, when possible, and sagittal otoliths were removed, rinsed, and stored in coin envelopes until processed.

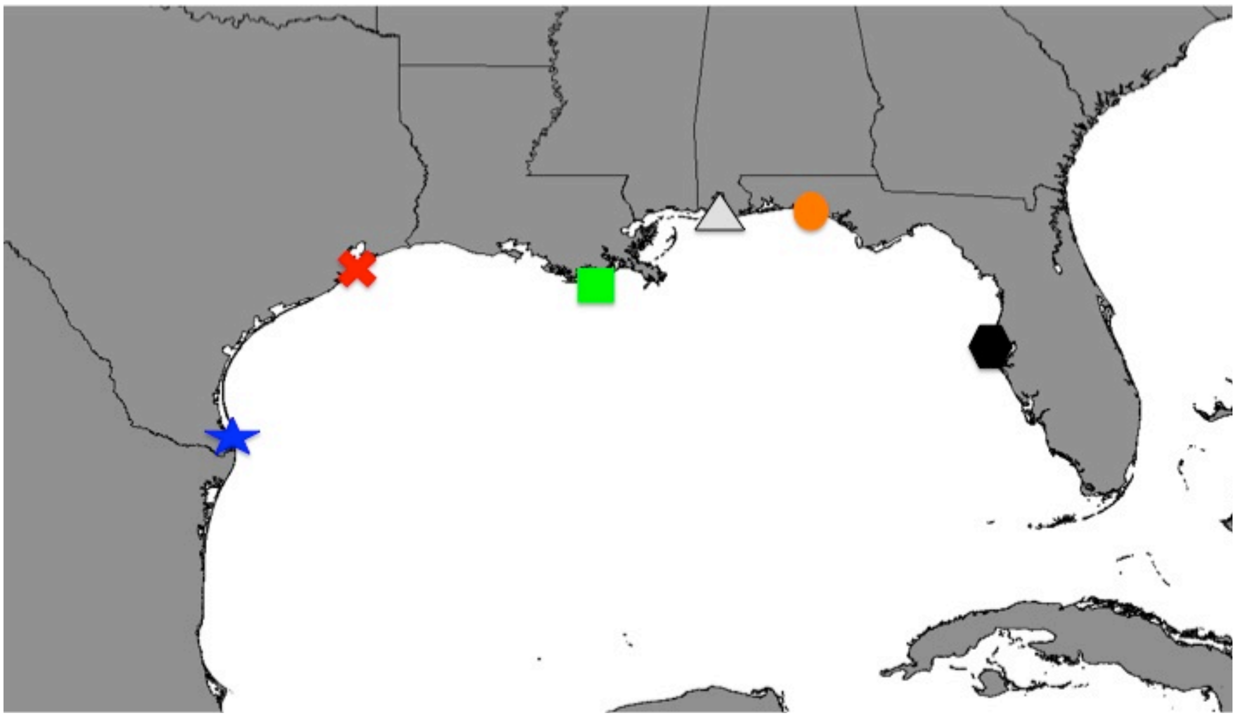

Figure 3.1. Red snapper (*Lutjanus campechanus*) were sampled from six recreational fishing regions in the U.S. waters of the Gulf of Mexico; South Texas (blue star), North Texas (red x), Louisiana (green square), Alabama (gray triangle), Northwest Florida (orange circle), and Central Florida (black hexagon).

3.2.1 Otolith Processing and Aging

The left sagittal otoliths were sectioned in a transverse plane following the methods of Cowan et al. (1995). Sections were made using the Hillquist model 800 thin-sectioning machine equipped with a diamond embedded wafering blade and precision grinder (Cowan et al. 1995). When the left otolith was unavailable or damaged, the right otolith was sectioned. Otolith sections were read under a dissecting microscope with transmitted light and a polarized light filter at 20x to 64x magnification. Counts of opaque annuli were made along the ventral margin of the sulcus acousticus from the core to the proximal edge (Wilson and Nieland 2001). The appearance of the otolith's margin, known as edge condition, was coded according to Beckman et al. (1989). Annulus counts were performed by two independent readers without knowledge of date or location of capture or morphometric data. When initial counts disagreed, annuli were counted a second time. In instances where a consensus between the two readers could not be reached, the annulus counts from the more experienced reader were reported. Precision between readers was evaluated with the coefficient of variation (CV), index of precision (D) (Chang 1982), and average percent error (APE) (Beamish and Fournier 1981). Ages of red snapper were estimated from the number of opaque annuli, assumed birthdate, and capture date, following the equation described by Wilson and Nieland (2001):

$$\text{Age (days)} = -182 + (\textit{annulus count} \times 365) + ((m-1) \times 30) + d, \qquad (1)$$

where m = the ordinal number (1-12) of month of capture; and d = the ordinal number (1-31) of the day of the month of capture. It was assumed for red snapper in the northern GOM that annulus formation begins on 1 January, with a uniform birthdate of 1 July. To account for the uniform birthdate, 182 days were subtracted from each age estimate. To assign a biological age in years, the age in days was divided by 365.

3.2.2 Size and Age Distributions

Analysis of variance (ANOVA) was used to compare mean total length (TL), total weight (TW), and age among regions (SAS Institute 2008). Total length, TW, and age were first ln-transformed to meet the assumptions of normality and homogeneity of variance. Tukey's Studentized Range (HSD) Test was used for pair-wise comparison of the means. Size and age distributions were compared pair-wise by region with the Kolmogorov-Smirnov two-sample test (Tate and Clelland, 1957). A chi-squared (χ^2) test was used to determine if sex ratios differed from a 1:1 ratio overall and among regions. For all statistical tests, significance was measured at an alpha level of 0.05.

3.2.3 Growth

Traditional allometric relationships of fish length to weight were fitted with linear regression to the model TL = aTW^b from ln-transformed data for all fish combined and by region. Analysis of Covariance (ANCOVA) was used to compare, among regions, the linearized slopes and intercepts, corresponding to the exponent b and multiplier a in the exponential length-weight model. For all statistical tests, significance was measured at an alpha level of 0.05.

To examine growth differences among red snapper from the six regions, weighted mean size-at-age was compared for the most common ages (3-7 yrs) using ANOVA with a Tukey's Studentized (HSD) Adjustment for post-hoc comparisons. To compare red snapper growth among the regions, observed TL at age and TW at age were modeled with the von Bertalanffy growth equations. Growth models were calculated for all fish combined and separately by region and sex. For all von Bertalanffy equations, no y-intercepts for t_0 were specified and models were forced through 0 for comparison purposes due to of a lack of smaller, younger individuals in all sample populations. Von Bertalanffy growth models were fitted with nonlinear regression by least squares (SAS Institute 2008) in the forms:

$$TL_t=L_\infty(1-e^{-k(t)}) , \qquad (2)$$

$$TW_t=W_\infty(1-e^{-k(t)})^b , \qquad (3)$$

where: TL_t = TL at age t; TW_t = TW at age t;

L_∞ = the TL asymptote; W_∞ = the TW asymptote;

k = the growth coefficient;   t = age in yr;

b = exponent derived from the length-weight regressions.

Likelihood ratio tests (Cerrato 1990) were used to test for differences among regions in von Bertalanffy models and in growth parameter estimates using the solver function in Microsoft Excel 2011 (Haddon 2001). For all statistical tests, significance was measured at an alpha level of 0.05.

3.3 Results

During the summers of 2009 and 2010, 1808 red snapper from six major recreational regions of the GOM were sampled for morphometric data and sagittal otoliths (Table 3.1): 348 specimens from South Texas, 224 specimens from North Texas, 268 from Louisiana, 204 from Alabama, 463 specimens from Northwest Florida, 301 from Central Florida. Overall, the samples included 937 females, 761 males, and 109 individuals of unknown sex (Table 3.1), with a male-to-female ratio of 0.81:1.00. A chi-square test indicated a significant difference in the male-to-female ratio across all regions (χ^2=21.68, p<0.0001). The regions with sex ratios that are significantly different from 1:1 are South Texas, Northwest Florida, and Central Florida (Table 3.2).

Table 3.1. Numbers of red snapper, *Lutjanus campechanus*, sampled from six major recreational regions of the Gulf of Mexico.

Region	Males	Females	Unknown Sex	Total
South Texas	134	191	23	348
North Texas	111	93	20	224
Louisiana	131	132	5	268
Alabama	93	108	3	204
Northwest Florida	186	254	23	463
Central Florida	105	161	34	301
Total	761	938	108	1808

Table 3.2. Chi-squared (χ^2) analysis of male-to-female ratios (M:F) of red snapper, *Lutjanus campechanus*, sampled from six major recreational regions of the Gulf of Mexico.

Region	M:F	χ^2	P value
South Texas	0.70:1	12.20	0.0022
North Texas	1.19:1	3.14	0.2076
Louisiana	0.99:1	0.10	0.9508
Alabama	0.86:1	2.26	0.3234
Northwest Florida	0.73:1	13.47	0.0012
Central Florida	0.65:1	14.85	0.0006

3.3.1 Size Distributions

Total lengths of all red snapper ranged from 389 to 900 mm with a mean of 540.19 ± 2.17 mm (Fig 3.2A). The minimum, maximum and mean total length (mm) of red snapper from each region is reported in Table 3.3. Significant differences were noted among the mean total lengths of red snapper from each region (Figure 3.4 and Table 3.4). Red snapper from Alabama had the largest mean total length, which was significantly larger than all of the other regions, and red snapper from Northwest Florida had the significantly smallest mean total length (Table 3.4). Mean total length of red snapper from South Texas and Louisiana red snapper were significantly larger than red snapper from North Texas, Northwest Florida and Central Florida, but not significantly different from each other (Table 3.4). Mean total length of red snapper from North Texas and Central Florida were not significantly different from each other (Table 3.4).

The total length frequency distributions were significantly different among all of the regions except for South Texas and Louisiana (P>KSa: p=0.1023) and North Texas and Central Florida (P>KSa: p=0.1759). Northwest Florida had the largest proportion of small (<550 mm) red snapper (Fig 3.3). No significant differences in the total length frequency distributions and means were found between the sexes (P>KSa: p=0.4922 and p=0.6781, respectively).

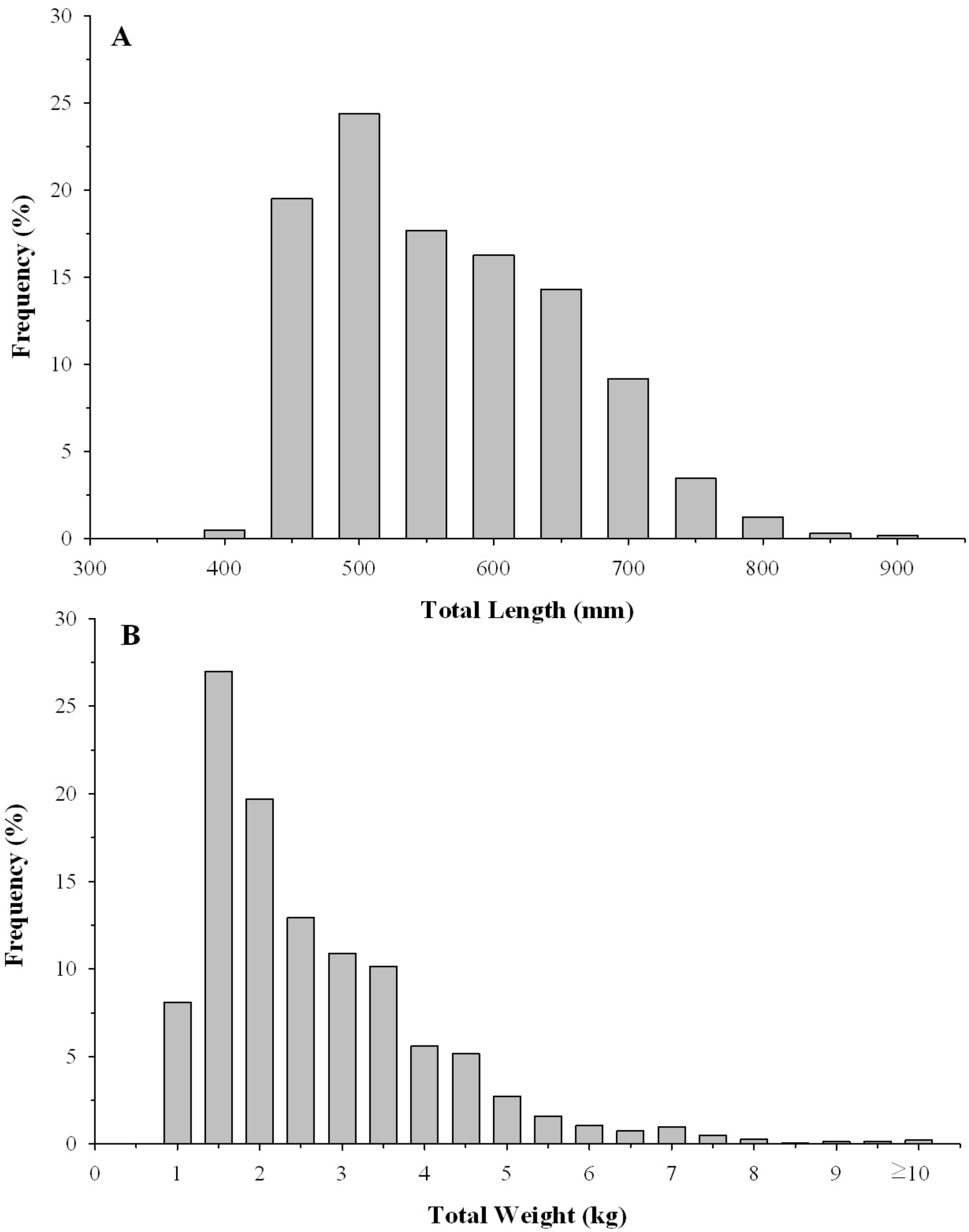

Figure 3.2. Distributions of A. total length (mm; n= 1759) and B. total weight (kg; n=1545) for red snapper, *Lutjanus campechanus*, sampled from six recreational fishing regions in the Gulf of Mexico.

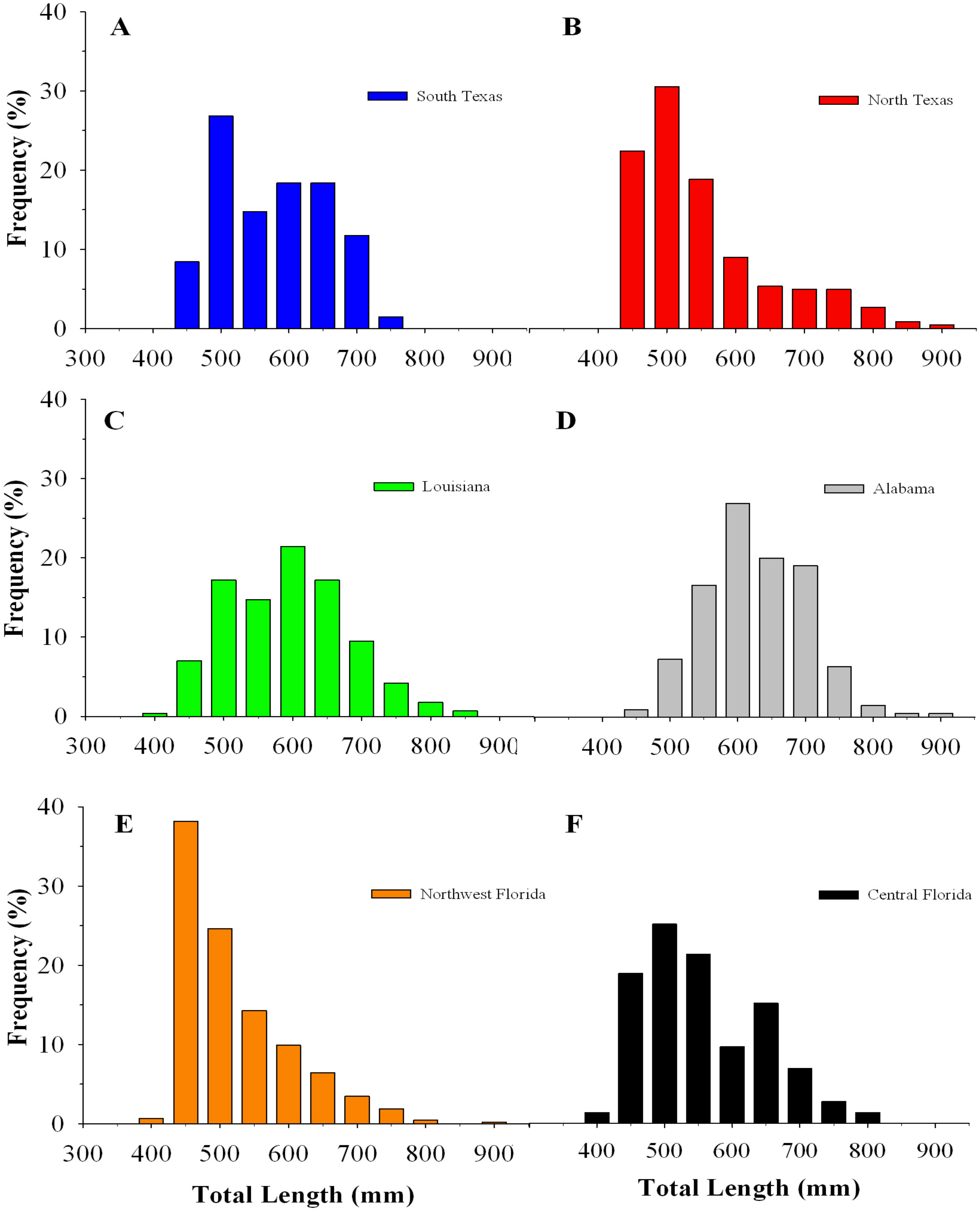

Figure 3.3. Distributions of total length (mm) for red snapper, *Lutjanus campechanus*, sampled from six recreational fishing regions in the Gulf of Mexico: A. South Texas (n=332), B. North Texas (n=223), C. Louisiana (n=268), D. Alabama (n=204), E. Northwest Florida (n=435), and F. Central Florida (n=298).

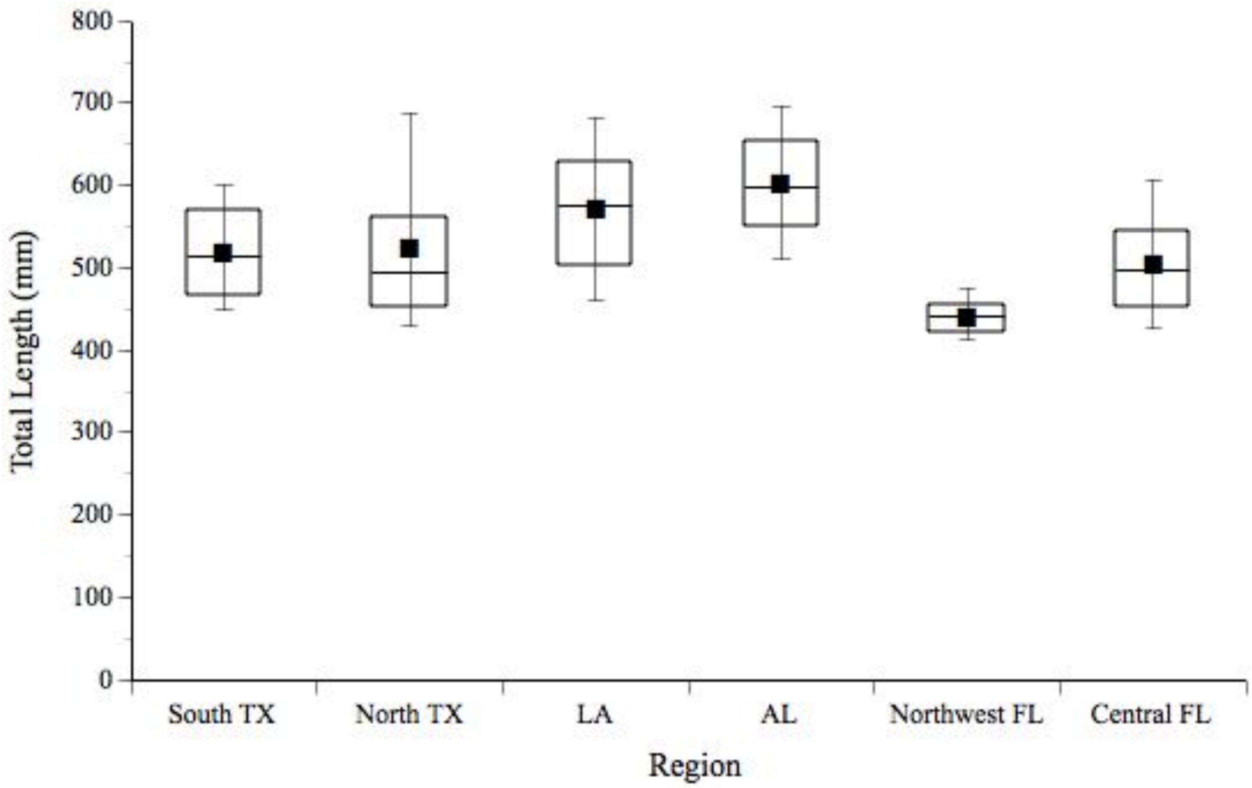

Figure 3.4. Box plots of the total length (mm) of red snapper, *Lutjanus campechanus*, sampled from six recreational fishing regions in the Gulf of Mexico: South Texas (n=332), North Texas (n=223), Louisiana (n=268), Alabama (n=204), Northwest Florida (n=435), and Central Florida (n=298). Boxes signify the 75th and 25th percentiles, black squares signify the means, and the line within each box signifies the median. The whiskers extend from the 10th percentile to the 90th percentile.

Table 3.3. Minimum, maximum, and mean ± standard error of total length (mm) of red snapper, *Lutjanus campechanus*, sampled from six recreational fishing regions in the Gulf of Mexico: South Texas (n=332), North Texas (n=223), Louisiana (n=268), Alabama (n=204), Northwest Florida (n=435), and Central Florida (n=298).

Region	Minimum TL	Maximum TL	Mean TL ± Standard Error
South Texas	406	722	552.10 ± 4.34
North Texas	410	900	525.94 ± 6.63
Louisiana	400	821	560.87 ± 5.24
Alabama	426	880	604.19 ± 5.26
Northwest Florida	389	880	497.15 ± 3.90
Central Florida	394	780	530.43 ± 5.08

Table 3.4. Least square means with Tukey's adjustment on the mean total length (mm) of red snapper, *Lutjanus campechanus*, from six recreational fishing regions in the Gulf of Mexico: South Texas (n=332), North Texas (n=223), Louisiana (n=268), Alabama (n=204), Northwest Florida (n=435), and Central Florida (n=298).

	South Texas	**North Texas**	**Louisiana**	**Alabama**	**Northwest Florida**
North Texas	0.0006				
Louisiana	0.1781	<0.0001			
Alabama	<0.0001	<0.0001	0.0001		
Northwest Florida	<0.0001	0.0004	<0.0001	<0.0001	
Central Florida	0.0055	0.9615	<0.0001	<0.0001	<0.0001

Total weights of all red snapper ranged from 0.64 to 12.7 kg with a mean of 2.40 ± 0.04 kg (Fig 3.2B). The minimum, maximum and mean total length (mm) of red snapper from each region is reported in Table 3.5. Mean total weight of red snapper from Alabama was significantly heavier than red snapper from all of the other regions (Figure 3.6 and Table 3.6). Mean total weights of red snapper from South Texas and Louisiana were significantly larger than red snapper from North Texas, Northwest Florida, and Central Florida, which were not significantly different from each other (Table 3.6).

Table 3.5. Minimum, maximum, and mean ± standard error of total weight (kg) of red snapper, *Lutjanus campechanus*, sampled from six recreational fishing regions in the Gulf of Mexico: South Texas (n=332), North Texas (n=223), Louisiana (n=268), Alabama (n=204), Northwest Florida (n=435), and Central Florida (n=298).

Region	**Minimum TW**	**Maximum TW**	**Mean TW ± Standard Error**
South Texas	0.64	9.22	2.54 ± 0.6
North Texas	0.84	10.25	2.18 ± 0.11
Louisiana	0.87	8.71	2.45 ± 0.10
Alabama	1.04	12.7	3.28 ± 0.10
Northwest Florida	0.64	9.16	2.10 ± 0.08
Central Florida	0.65	7.52	2.21 ± 0.08

Table 3.6. Least square means with Tukey's adjustment on the mean total weight (kg) of red snapper, *Lutjanus campechanus*, from six recreational fishing regions in the Gulf of Mexico: South Texas (n=318), North Texas (n=203), Louisiana (n=79), Alabama (n=178), Northwest Florida (n=388), and Central Florida (n=265).

	South Texas	North Texas	Louisiana	Alabama	Northwest Florida
North Texas	0.0005				
Louisiana	1.0000	0.0017			
Alabama	<0.0001	<0.0001	<0.0001		
Northwest Florida	<0.0001	0.7450	<0.0001	<0.0001	
Central Florida	0.0031	0.9824	0.0087	<0.0001	0.1929

The total weight distributions were significantly different among all of the regions except for North Texas and Northwest Florida (P>KSa: p=0.0552) and North Texas and Central Florida (P>KSa: p=0.1025). North Texas and Northwest Florida had the largest proportions of small (<2.5 kg) red snapper (Fig 3.5). No significant differences in the total weight frequency distributions and means were found between the sexes (P>KSa: p=0.6548 and Tukey's p=0.9245, respectively).

Significant differences in red snapper TL-TW regression models were detected among the regions (ANCOVA test of homogeneity of slopes, $F_{5;1498}=2.86$; p=0.0141; $r^2=0.9174$; ANCOVA test of equal intercepts, $F_{5;1498}=2.95$; p=0.0117; $r^2=0.9174$); therefore separate models were fitted for each region (Fig 3.7). No significant differences occurred between the TL-TW regressions for males and females (ANCOVA test of homogeneity of slopes, $F_{1;1504}=0.11$; p=0.8918; $r^2=0.9126$; ANCOVA test of equal intercepts, $F_{1;1504}=0.13$; p=0.8748; $r^2=0.9126$). The TL-TW equations for each region are given in Table 3.7.

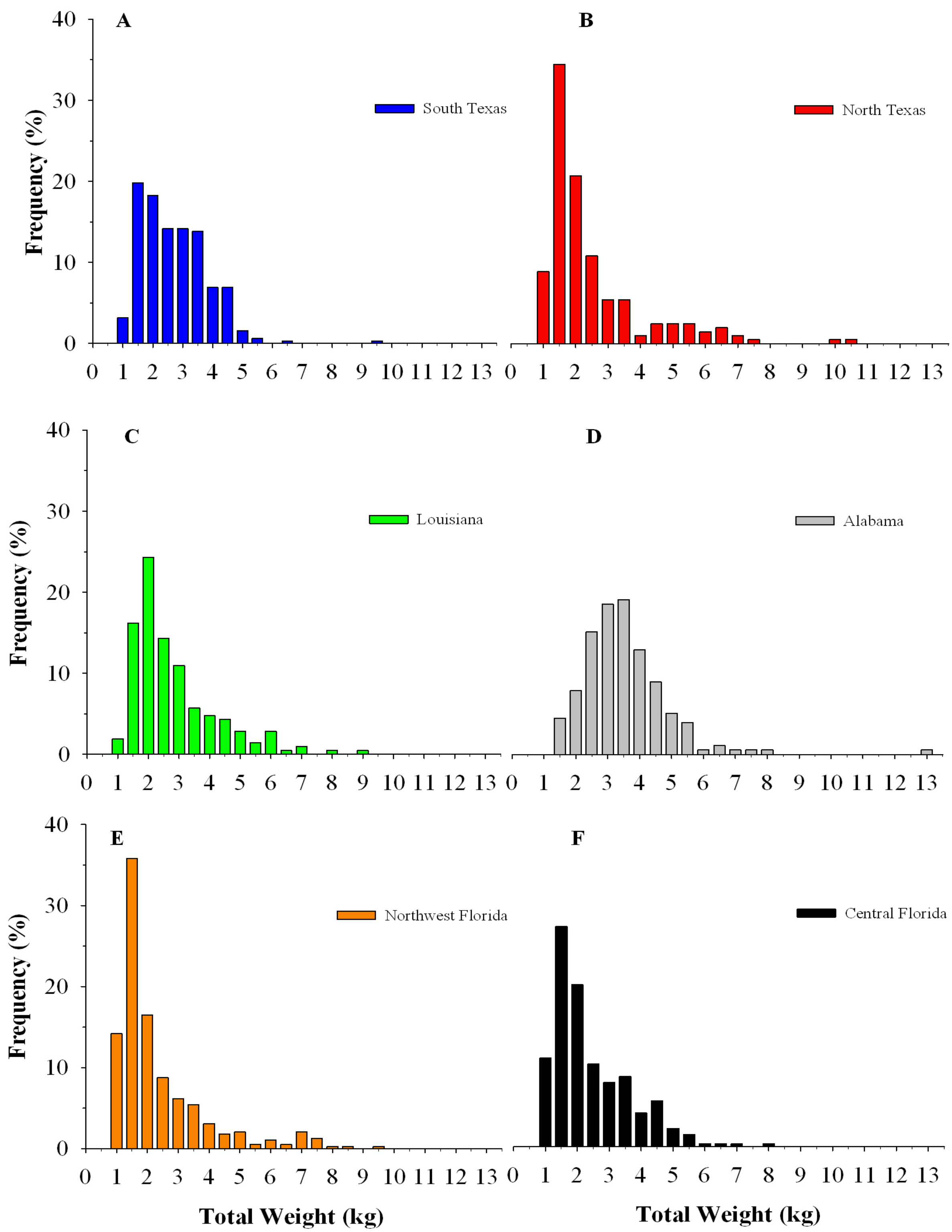

Figure 3.5. Distributions of total weight (kg) for red snapper, *Lutjanus campechanus*, sampled from six recreational fishing regions in the Gulf of Mexico: A. South Texas (n=318), B. North Texas (n=203), C. Louisiana (n=193), D. Alabama (n=178), E. Northwest Florida (n=388), and F. Central Florida (n=265).

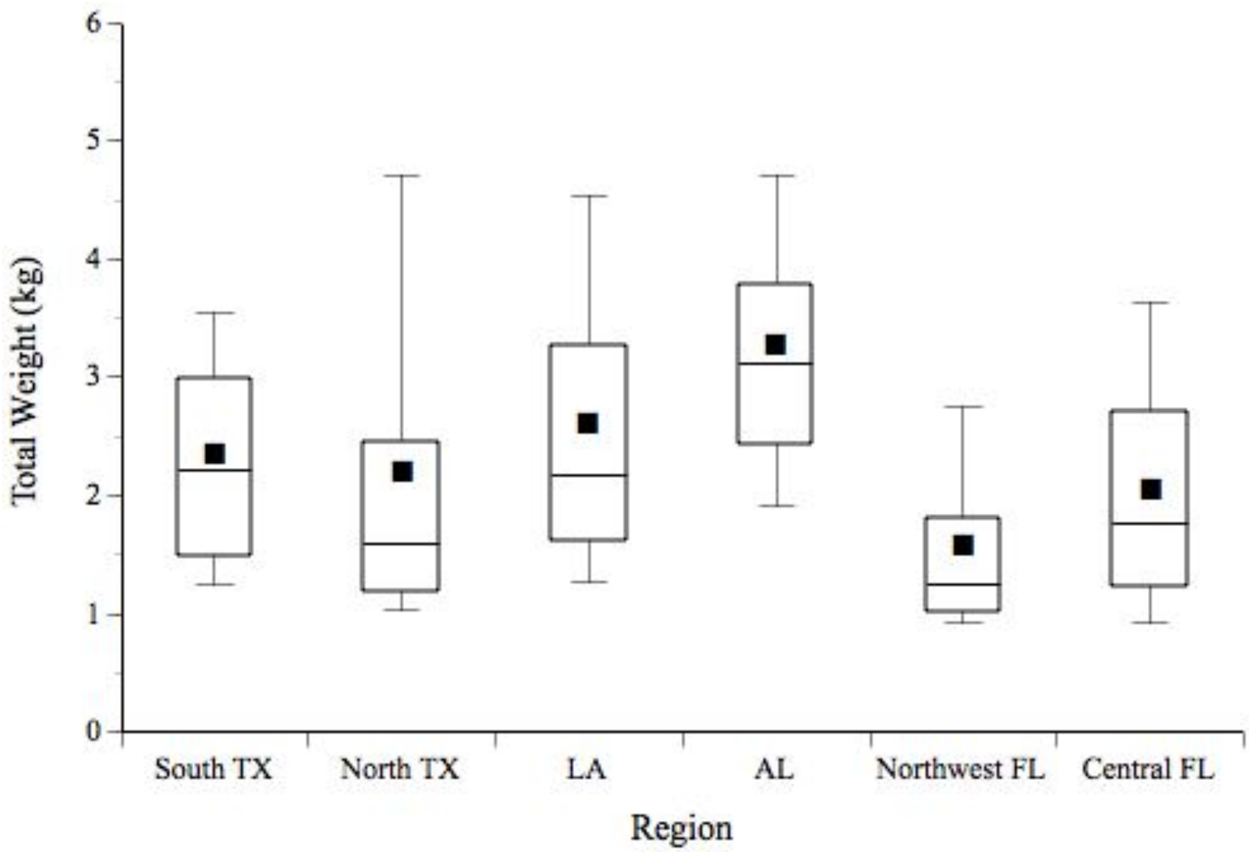

Figure 3.6 Box plots of the total weight (kg) of red snapper, *Lutjanus campechanus*, sampled from six recreational fishing regions in the Gulf of Mexico: South Texas (n=318), North Texas (n=203), Louisiana (n=79), Alabama (n=178), Northwest Florida (n=388), and Central Florida (n=265). Boxes signify the 75th and 25th percentiles, black squares signify the means, and the line within each box signifies the median. The whiskers extend from the 10^{th} percentile to the 90^{th} percentile.

Table 3.7. Total weight – total length regression models for red snapper, *Lutjanus campechanus*, sampled from three habitats on Louisiana's continental shelf.

Region	**TW-TL equation**
South Texas	$TW = 2.49 \times 10^{-8}(TL)^{2.90}$
North Texas	$TW = 7.85 \times 10^{-9}(TL)^{3.08}$
Louisiana	$TW = 1.66 \times 10^{-8}(TL)^{2.97}$
Alabama	$TW = 3.61 \times 10^{-8}(TL)^{2.85}$
Northwest Florida	$TW = 1.20 \times 10^{-8}(TL)^{3.02}$
Central Florida	$TW = 5.11 \times 10^{-9}(TL)^{3.15}$

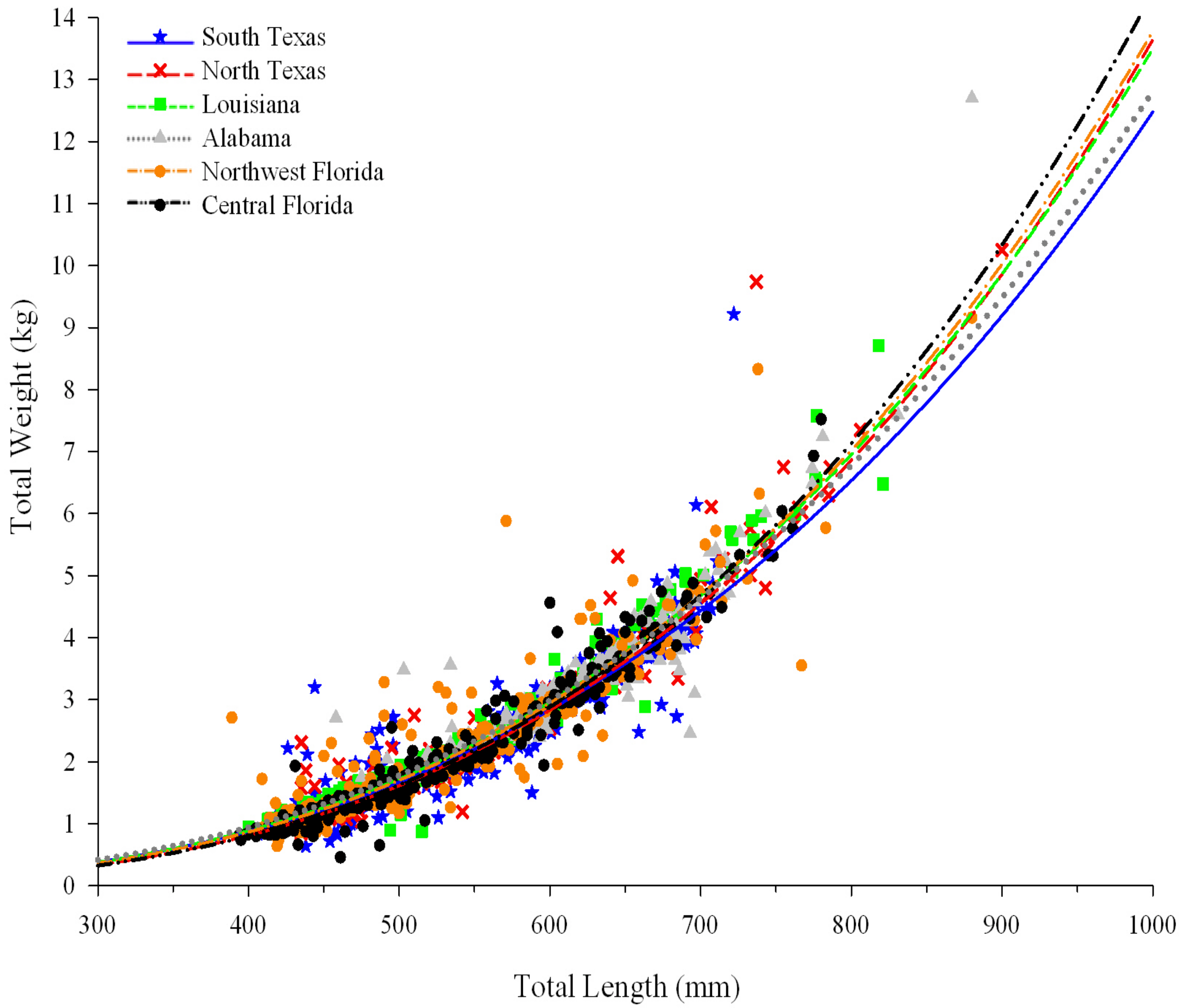

Figure 3.7. Scatterplot of the relationships between observed total weight (kg) and total length (mm) of red snapper, *Lutjanus campechanus*, from six recreational fishing regions of the Gulf of Mexico: A. South Texas (n=318), B. North Texas (n=203), C. Louisiana (n=193), D. Alabama (n=178), E. Northwest Florida (n=388), and F. Central Florida (n=265).

The TL-TW model for red snapper from Central Florida exhibited the fastest growth coefficient (*b*), however it was not significantly greater than the estimated values of *b* for the North Texas and Northwest Florida models (Table 3.8 and Fig 3.7). The South Texas and Alabama TL-TW models displayed the smallest estimates of *b* (Table 3.7). The intercept estimate of *a* from the Central Florida model was significantly smaller than the estimates of *a* from the South Texas, Louisiana, and Alabama models (Table 3.8). No significant difference was noted among the estimates of *a* from the Central Florida, Northwest Florida and North Texas models (Table 3.8).

Table 3.8. ANCOVA results for A. homogeneity of slopes and B. equal intercepts for the total length (mm) – total weight (kg) regression models of red snapper, *Lutjanus campechanus*, sampled from six regions of the Gulf of Mexico: South Texas (n=318), North Texas (n=203), Louisiana (n=193), Alabama (n=178), Northwest Florida (n=388), and Central Florida (n=265).

A. Homogeneity of Slopes

	South Texas	North Texas	Louisiana	Alabama	Northwest Florida
North Texas	0.0317				
Louisiana	0.4300	0.1939			
Alabama	0.6300	0.0306	0.2742		
Northwest Florida	0.1390	0.3967	0.5991	0.1044	
Central Florida	0.0032	0.4383	0.0499	0.0040	0.0882

B. Equal Intercepts

	South Texas	North Texas	Louisiana	Alabama	Northwest Florida
North Texas	0.0318				
Louisiana	0.4772	0.2204			
Alabama	0.5902	0.0279	0.2801		
Northwest Florida	0.1373	0.3962	0.5414	0.0943	
Central Florida	0.0030	0.4217	0.0397	0.0033	0.0822

3.3.2 Age Distributions

Ages were obtained from 1808 transverse otolith sections. After the initial reading, the readers agreed on 85.6% of the otoliths, with an APE of 1.77% (Table 3.9). After the second reading, the readers reached agreement for 91.9% of the otoliths, with an APE of 1.08% (Table 3.9). Overall, age of red snapper ranged from 2 to 33 yr (Table 3.10), with the majority (86.24%) of individuals between the ages of 3 and 5 yr (Fig 3.8A). The mean age was 4.51 ± 0.03 yr with few (3.5%) red snapper aged older than 6 yr (Fig 3.8A). The majority (89.02%) of the red snapper appear to be derived from the strong 2004, 2005 and 2006 year-classes (Fig 3.8B).

Table 3.9. Differences between the two readers in average percent error (APE), coefficient of variation (CV), index of precision (D), percentages of agreement (O) for opaque annuli counts, and percentages of differences in age estimates (±1, 2, and 3 or more years) in red snapper, *Lutjanus campechanus*, otoliths after the first and second readings (n=1808).

	1st reading	**2nd reading**
APE	1.77 %	1.08 %
CV	0.0177	0.0108
D	0.0125	0.0076
O	85.6%	91.9%
±1	13.54%	6.91%
±2	0.59%	1.00%
≥ ±3	0.18%	0.18%

The minimum, maximum and mean age (yr) of red snapper from each region is reported in Table 3.10. Red snapper from the two Florida regions had significantly smaller mean ages then red snapper from the other four regions (Fig 3.10 and Table 3.11). The age frequency distributions were significantly different among all of the regions, except for the regions with the highest proportion of older fish: North Texas and Louisiana (P>KSa: p=0.4585), South Texas and Alabama (P>KSa: p=0.2632), Louisiana and Alabama (P>KSa: p=0.0532), as well as between the two regions with the highest proportion of young fish: North and Central Florida

(P>KSa: p=0.0765). No significant differences in the age distributions and means were found between the sexes (P>KSa: p=0.7691 and Tukey's p=0.7627, respectively).

Table 3.10. Minimum, maximum, and mean ± standard error of age (yr) of red snapper, *Lutjanus campechanus*, sampled from six recreational fishing regions in the Gulf of Mexico: South Texas (n=332), North Texas (n=223), Louisiana (n=268), Alabama (n=204), Northwest Florida (n=435), and Central Florida (n=298).

Region	Minimum Age	Maximum Age	Mean Age ± Standard Error
South Texas	3	13	4.86 ± 0.06
North Texas	3	33	4.78 ± 0.15
Louisiana	3	21	4.72 ± 0.10
Alabama	3	16	4.79 ± 0.08
Northwest Florida	2	9	4.17 ± 0.05
Central Florida	2	10	4.06 ± 0.06

3.3.3 Growth

There were significant differences among the regions in the mean size-at-age of red snapper (Fig 3.11). Red snapper from South Texas and Northwest Florida were consistently smaller in total length at age than red snapper from the other regions (Fig 3.11A and Table 3.12). At ages 4, 5, and 6, red snapper from South Texas and Northwest Florida were significantly smaller in mean total length than red snapper from Louisiana, Alabama and Central Florida (Fig 3.11A, Table 3.12). At ages 4 and 5, red snapper from North Texas were significantly smaller than red snapper from Louisiana, Alabama, and Central Florida, but not significantly different from South Texas and Northwest Florida red snapper (Fig 3.11A, Table 3.12). Also at ages 4 and 5, red snapper from Alabama were significantly larger than red snapper from all of the other regions (Table 3.12). No significant differences in mean total length at age were observed between red snapper from Louisiana and Central Florida (Table 3.12). Statistical comparisons of size-at-age for red snapper older than age 7 were not possible due to insufficient sample size.

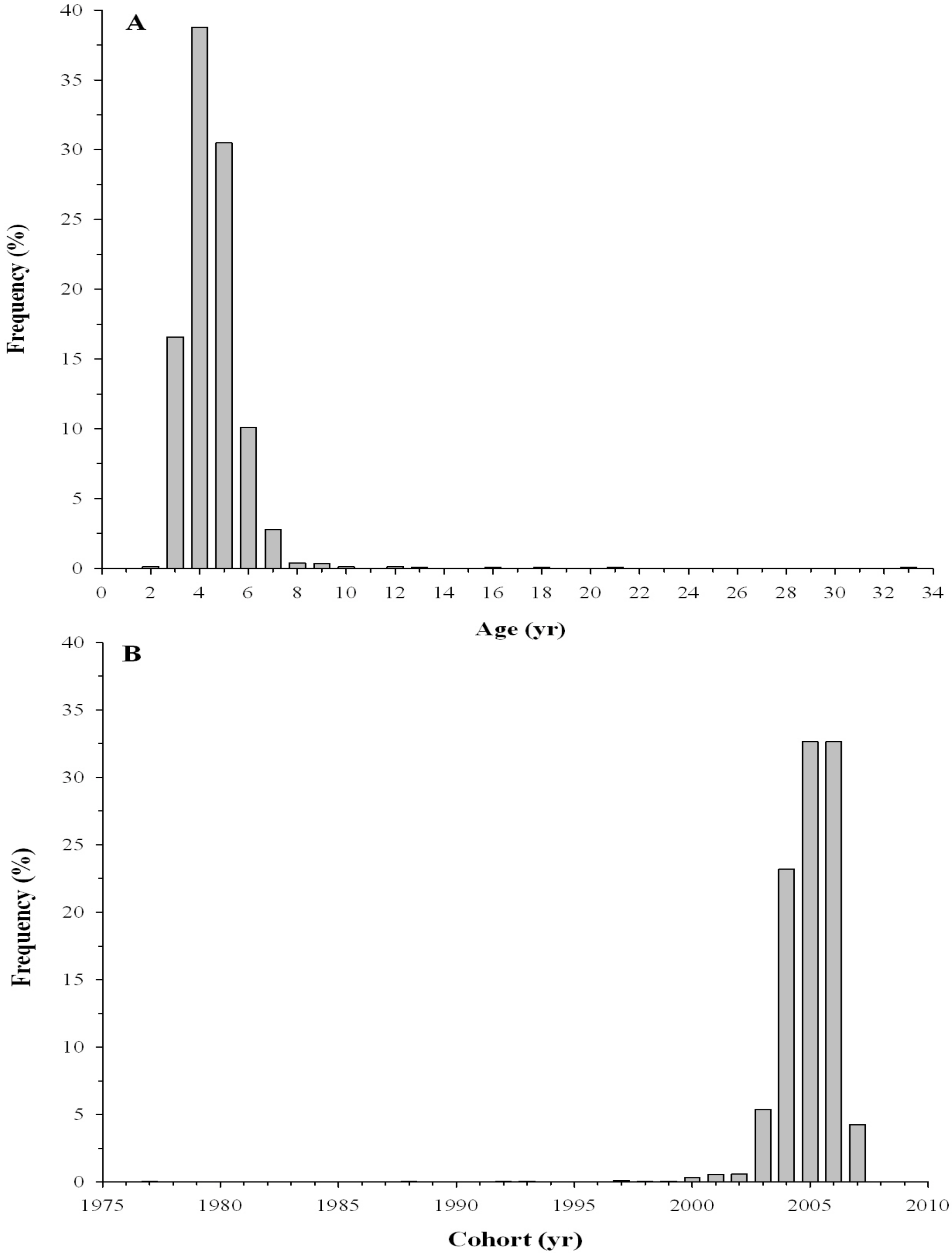

Figure 3.8. Distributions of A. age (yr) and B. cohort (yr) for red snapper, *Lutjanus campechanus*, sampled from six recreational fishing regions in the Gulf of Mexico (n=1808), where cohort association was estimated by back calculating age from Equation (1).

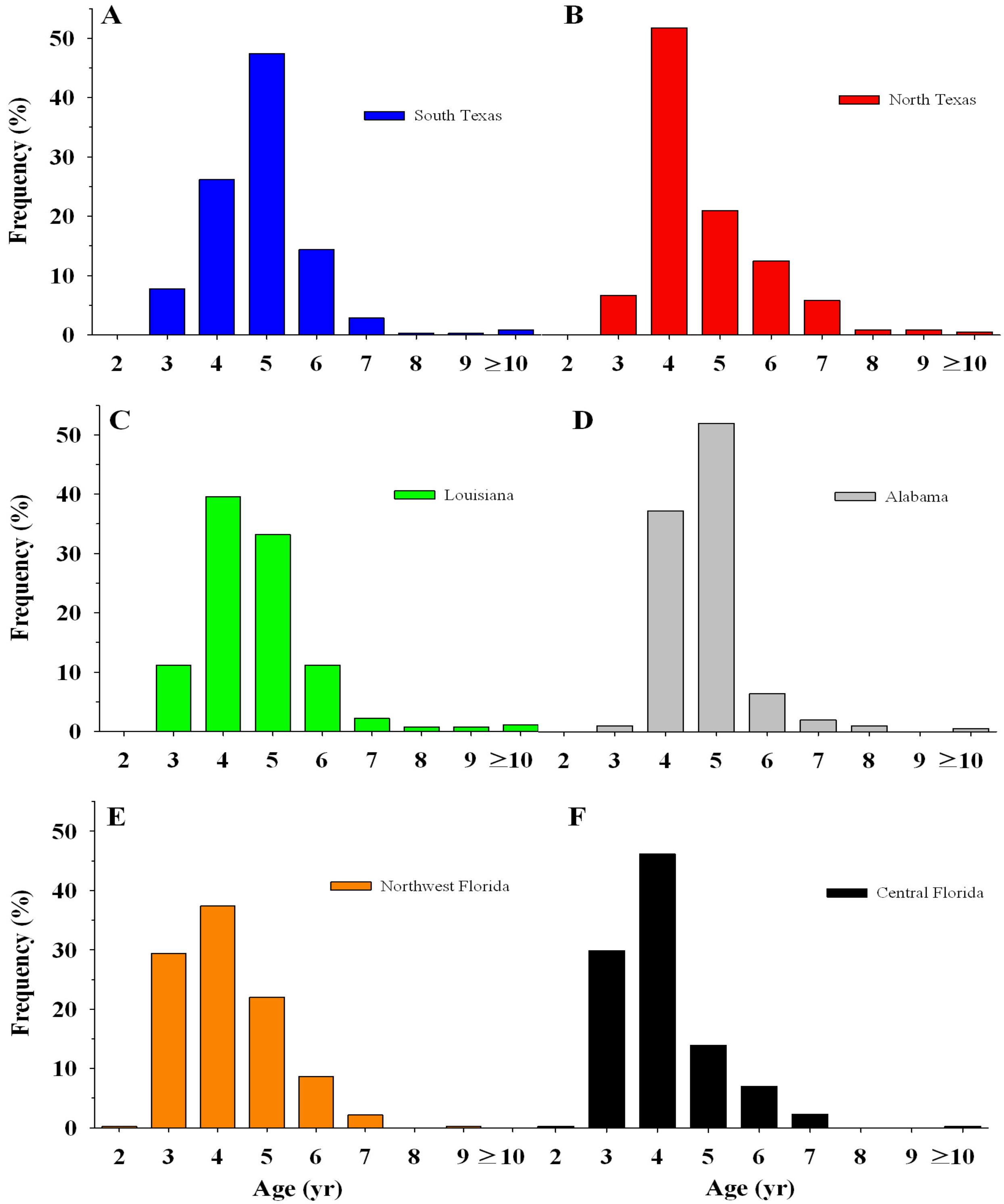

Figure 3.9. Distributions of age in years for red snapper, *Lutjanus campechanus*, sampled from six recreational fishing regions in the Gulf of Mexico: A. South Texas (n=348), B. North Texas (n=224), C. Louisiana (n=268), D. Alabama (n=204), E. Northwest Florida (n=463), and F. Central Florida (n=301).

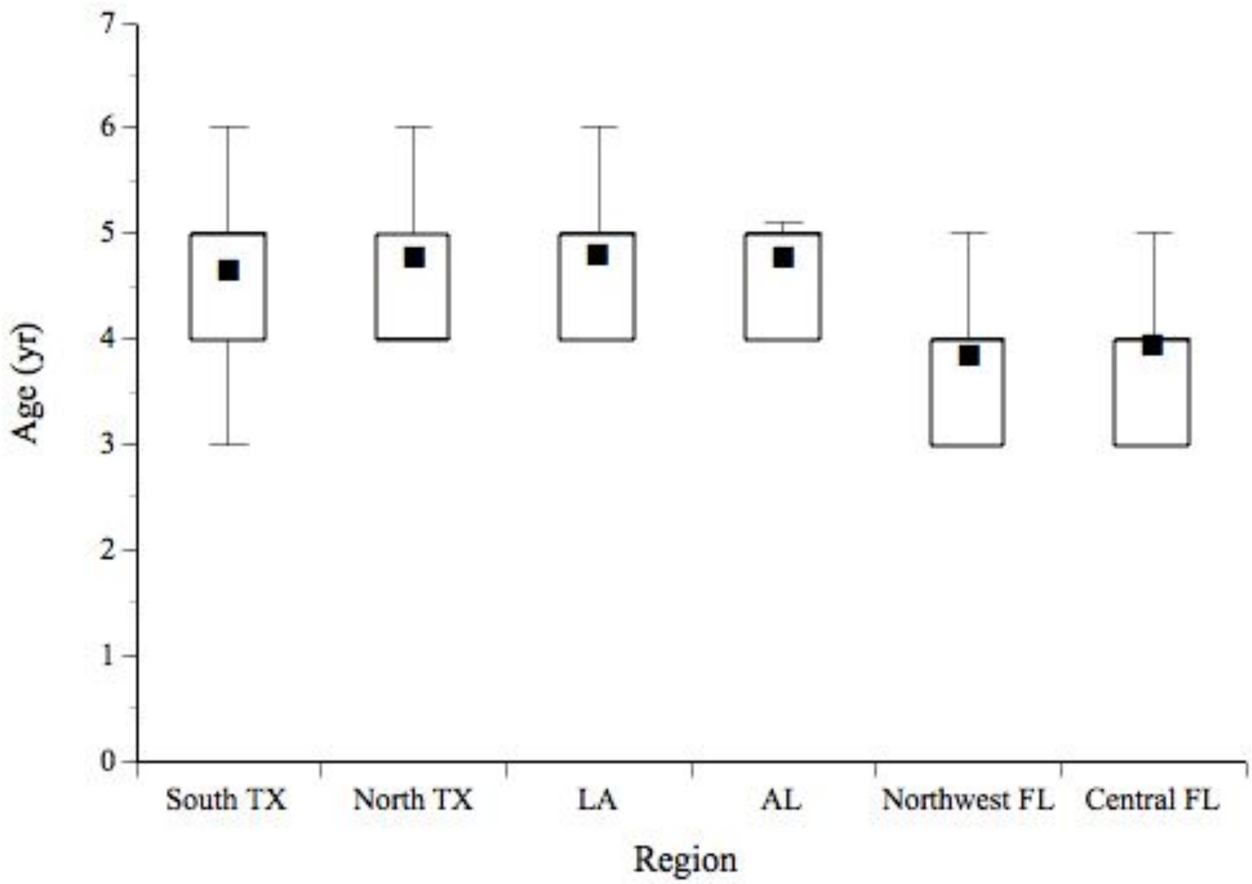

Figure 3.10. Box plots of the age (yr) of red snapper, *Lutjanus campechanus*, sampled from six recreational fishing regions in the Gulf of Mexico: South Texas (n=348), North Texas (n=224), Louisiana (n=154), Alabama (n=204), Northwest Florida (n=463), and Central Florida (n=301). Boxes signify the 75th and 25th percentiles, black squares signify the means, and the line within each box signifies the median. The whiskers extend from the 10th percentile to the 90th percentile.

Table 3.11. Least square means with Tukey's adjustment on the mean age (yr) of red snapper, *Lutjanus campechanus*, from six recreational fishing regions in the Gulf of Mexico: South Texas (n=348), North Texas (n=224), Louisiana (n=154), Alabama (n=204), Northwest Florida (n=463), and Central Florida (n=301).

	South Texas	**North Texas**	**Louisiana**	**Alabama**	**Northwest Florida**
North Texas	0.9786				
Louisiana	0.8156	0.9982			
Alabama	0.9933	1.0000	0.9939		
Northwest Florida	<0.0001	<0.0001	<0.0001	<0.0001	
Central Florida	<0.0001	<0.0001	<0.0001	<0.0001	0.8966

Table 3.12. Analyses of variance and Tukey's Studentized Range (HSD) Tests on red snapper, *Lutjanus campechanus*, mean total length (mm) at age (yr) by region of the Gulf of Mexico for the most common ages sampled (ages 3-7 yrs). Within each age, similar letters indicate no difference in mean total length (α = 0.05).

	ANOVA		Tukey's (HSD) comparisons of mean TL at age by region					
Age (yr)	**F**	**P**	**South Texas**	**North Texas**	**Louisiana**	**Alabama**	**Northwest Florida**	**Central Florida**
3	8.17	<0.0001	A	B	B	B	A	B
4	34.27	<0.0001	A	B	AD	C	B	D
5	18.59	<0.0001	A	B	C	D	AB	C
6	1.63	0.1557	A	B	B	B	A	AB
7	4.74	0.0015	A	A	AB	A	C	A

Red snapper from North Texas consistently weighed less at age than Louisiana and Alabama red snapper (Table 3.13). Except for at age 6, Northwest Florida red snapper weighed less at age than red snapper from Louisiana, Alabama, and Central Florida (Fig 3.11B and Table 3.13). At ages 4 and 5, red snapper from Alabama were significantly heavier than red snapper from all of the other regions (Table 3.13). Due to high variability, no significant differences in mean total weight at age 7 were observed among the regions (Fig 3.11B and Table 3.13).

Table 3.13. Analyses of variance and Tukey's Studentized Range (HSD) Tests on red snapper, *Lutjanus campechanus*, mean total weight (kg) at age (yr) by region of the Gulf of Mexico for the most common ages sampled (ages 3-7 yrs). Within each age, similar letters indicate no difference in mean total weight (α = 0.05).

	ANOVA		Tukey's (HSD) comparisons of mean TW at age by region					
Age (yr)	**F**	**P**	**South Texas**	**North Texas**	**Louisiana**	**Alabama**	**Northwest Florida**	**Central Florida**
3	8.58	<0.0001	A	AB	A	AB	B	AB
4	21.75	<0.0001	A	B	A	C	B	A
5	15.00	<0.0001	A	B	A	C	A	D
6	3.76	<0.0001	A	BD	BC	BC	C	D
7	0.90	0.4887	--	--	--	--	--	--

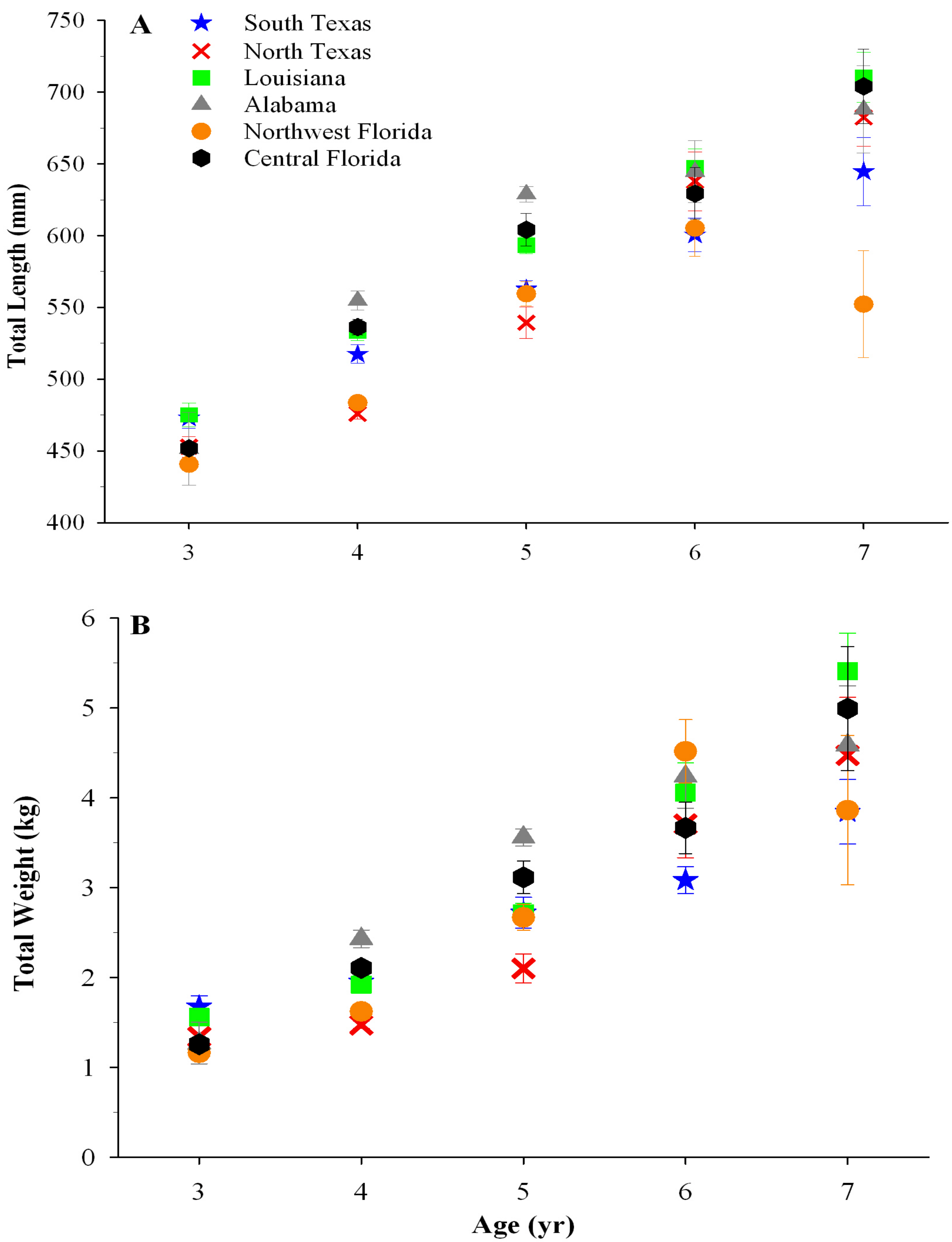

Figure 3.11. Mean A. total length at age and B. total weight at age of red snapper, *Lutjanus campechanus*, sampled from six recreational fishing regions in the Gulf of Mexico: South Texas, North Texas, Louisiana, Alabama, Northwest Florida, and Central Florida. Error bars represent standard error of the mean.

Red snapper growth, modeled from TL at age using the von Bertalanffy growth equation, was significantly different among the regions (likelihood ratio test; χ^2=280.95; df=10; p=1.64x10^{-54}) but not between the sexes (likelihood ratio test; χ^2=2.18; df=2; p=0.3362). Resultant TL von Bertalanffy growth equations are given in Table 3.14. All red snapper exhibited rapid growth until 6 to 8 years of age, after which growth slowed considerably (Figs 3.12 and 3.14).

Table 3.14. Von Bertalanffy growth models of total length at age for red snapper, *Lutjanus campechanus*, sampled from six recreational fishing regions in the Gulf of Mexico: South Texas (n=332), North Texas (n=223), Louisiana (n=268), Alabama (n=203), Northwest Florida (n=435), and Central Florida (n=298).

Region	**Von Bertalanffy TL Model**
South Texas	$TL_t=644.5(1 - e^{(-0.4189(t))})$
North Texas	$TL_t=908.2(1 - e^{(-0.1905(t))})$
Louisiana	$TL_t=771.0(1 - e^{(-0.2988(t))})$
Alabama	$TL_t=839.8(1 - e^{(-0.2747(t))})$
Northwest Florida	$TL_t=690.2(1 - e^{(-0.3219(t))})$
Central Florida	$TL_t=760.7(1 - e^{(-0.3103(t))})$

Von Bertalanffy growth models of red snapper TL at age were significantly different among all regions except for Louisiana and Central Florida (Table 3.15 and Fig 3.12). The L_∞ values were significantly different among all regions except for between North Texas and Alabama, as well as Louisiana and Central Florida (Table 3.15). The North Texas and Alabama growth models exhibited the largest L_∞ values, while the South Texas and Northwest Florida growth models exhibited the smallest L_∞ values (Fig 3.13). Both Texas models displayed *k* values that were significantly different from those in the models from the other four regions (Fig

3.13 and Table 3.15). The South Texas *k* value was significantly larger than the other regions' *k* values and the North Texas *k* value was significantly smaller than the other regions' *k* values (Table 3.15). No significant differences in *k* values were observed among Louisiana, Alabama, Northwest Florida and Central Florida (Table 3.15).

Table 3.15. Likelihood ratio test p-values for comparing red snapper, *Lutjanus campechanus*, total length von Bertalanffy growth models and parameters among six recreational fishing regions in the Gulf of Mexico: South Texas (n=332), North Texas (n=223), Louisiana (n=268), Alabama (n=203), Northwest Florida (n=435), and Central Florida (n=298).

	MODEL	L_∞	K
South Texas - North Texas	<0.0001	<0.0001	<0.0001
South Texas - Louisiana	<0.0001	<0.0001	<0.0001
South Texas - Alabama	<0.0001	<0.0001	0.0001
South Texas - Northwest Florida	<0.0001	0.0132	0.0003
South Texas - Central Florida	<0.0001	<0.0001	<0.0001
North Texas - Louisiana	<0.0001	<0.0001	<0.0001
North Texas - Alabama	<0.0001	0.0801	0.0002
North Texas - Northwest Florida	<0.0001	<0.0001	<0.0001
North Texas - Central Florida	<0.0001	<0.0001	<0.0001
Louisiana - Alabama	<0.0001	0.0388	0.5576
Louisiana - Northwest Florida	<0.0001	0.0003	0.2703
Louisiana - Central Florida	0.6244	0.7076	0.5933
Alabama - Northwest Florida	<0.0001	<0.0001	0.0232
Alabama - Central Florida	<0.0001	0.0077	0.0787
Northwest Florida - Central Florida	<0.0001	0.0003	0.5945

Von Bertalanffy growth models of red snapper TW at age (Fig 3.14) were also significantly different among all of the regions (likelihood ratio test; χ^2=228.49; df=10; p=1.78×10^{-43}) but not between the sexes (likelihood ratio test; χ^2=4.18; df=2; p=0.1237). Resultant TW von Bertalanffy growth equations are given in Table 3.16. Von Bertalanffy growth models of red snapper TW at age were significantly different among all regions (Table 3.17 and Fig 3.15). The W_∞ estimates were significantly different among all regions and the *k* estimates were significantly different among all regions except between North Texas and Alabama (Table 3.15). The Northwest Florida model had the largest W_∞ and smallest *k*, while the South Texas model had the smallest W_∞ and the largest *k* (Fig 3.15). The Central Florida model had the second smallest W_∞ and second largest *k* (Fig 3.15). The North Texas, Louisiana, and Alabama models had similar *k* values, ranging from 0.1856 to 0.2537 (Fig 3.15). The North Texas and Alabama models also had similar W_∞ values (10.71 and 12.70 kg, respectively), while the Louisiana and Central Florida models had similar W_∞ values (7.69 and 6.45 kg, respectively).

Table 3.16. Von Bertalanffy growth models of total weight at age for red snapper, *Lutjanus campechanus*, sampled from six recreational fishing regions in the Gulf of Mexico: (A) South Texas, (B) North Texas, (C) Louisiana, (D) Alabama, (E) Northwest Florida, and (F) Central Florida.

Region	Von Bertalanffy TW Model
South Texas	$TW_t=644.5(1 - e^{(-0.4189(t))})$
North Texas	$TW_t=10.57(1-e^{-0.1953(t)})^{3.08}$
Louisiana	$TW_t=7.69(1-e^{(-0.2537(t))})^{2.97}$
Alabama	$TW_t=12.75(1-e^{(-0.2033(t))})^{2.85}$
Northwest Florida	$TW_t=18.47(1-e^{(-0.1539(t))})^{3.02}$
Central Florida	$TW_t=6.45(1-e^{(-0.3104(t))})^{3.15}$

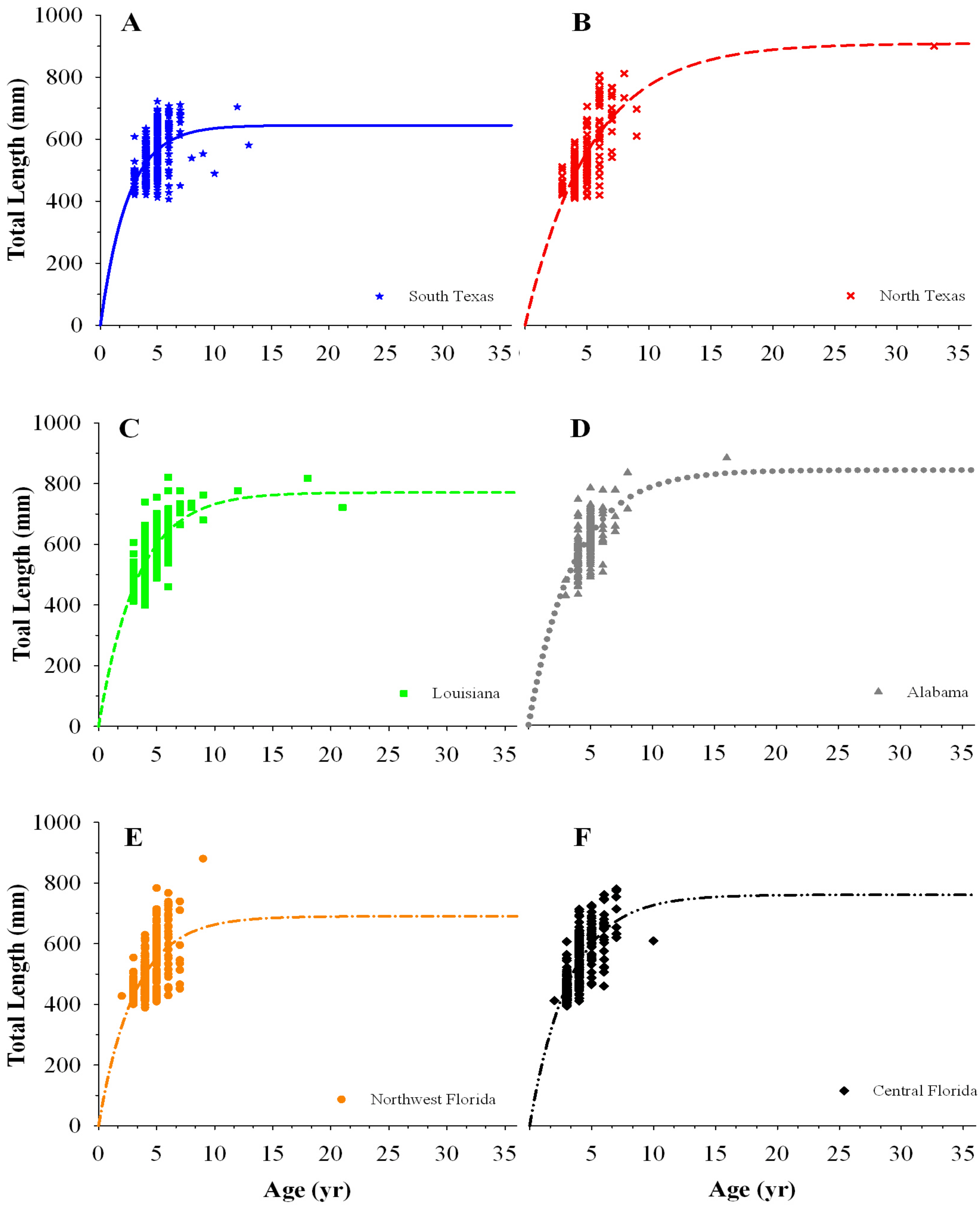

Figure 3.12. Observed total length at age and von Bertalanffy growth models for red snapper, *Lutjanus campechanus*, from six recreational fishing regions in the Gulf of Mexico: (A) South Texas (n=332), (B) North Texas (n=223), (C) Louisiana (n=268), (D) Alabama (n=203), (E) Northwest Florida (n=435), and (F) Central Florida (n=298).

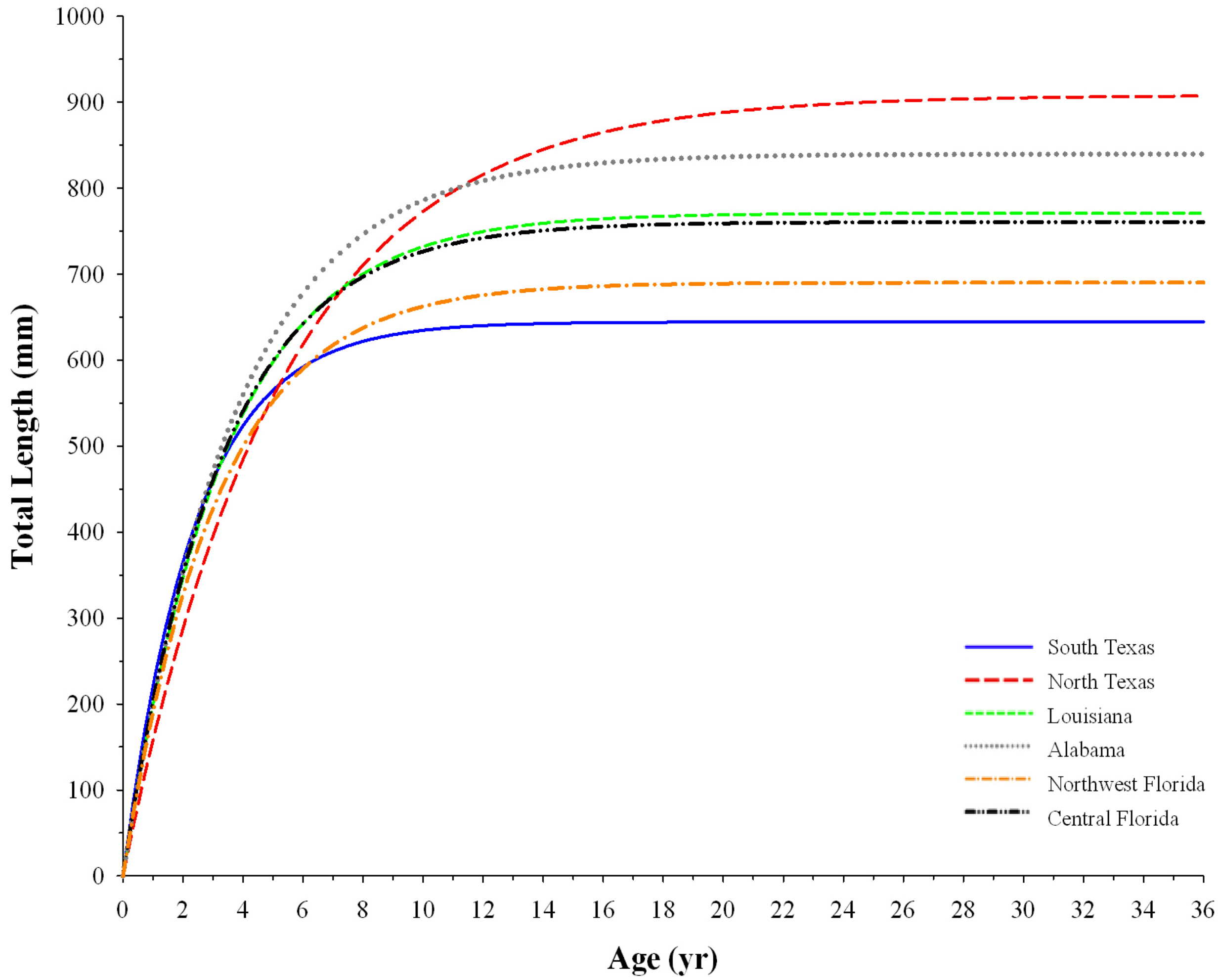

Figure 3.13. Comparative von Bertalanffy growth models for red snapper, *Lutjanus campechanus*, total length at age from six recreational fishing regions in the Gulf of Mexico: South Texas (n=332), North Texas (n=223), Louisiana (n=268), Alabama (n=203), Northwest Florida (n=435), and Central Florida (n=298).

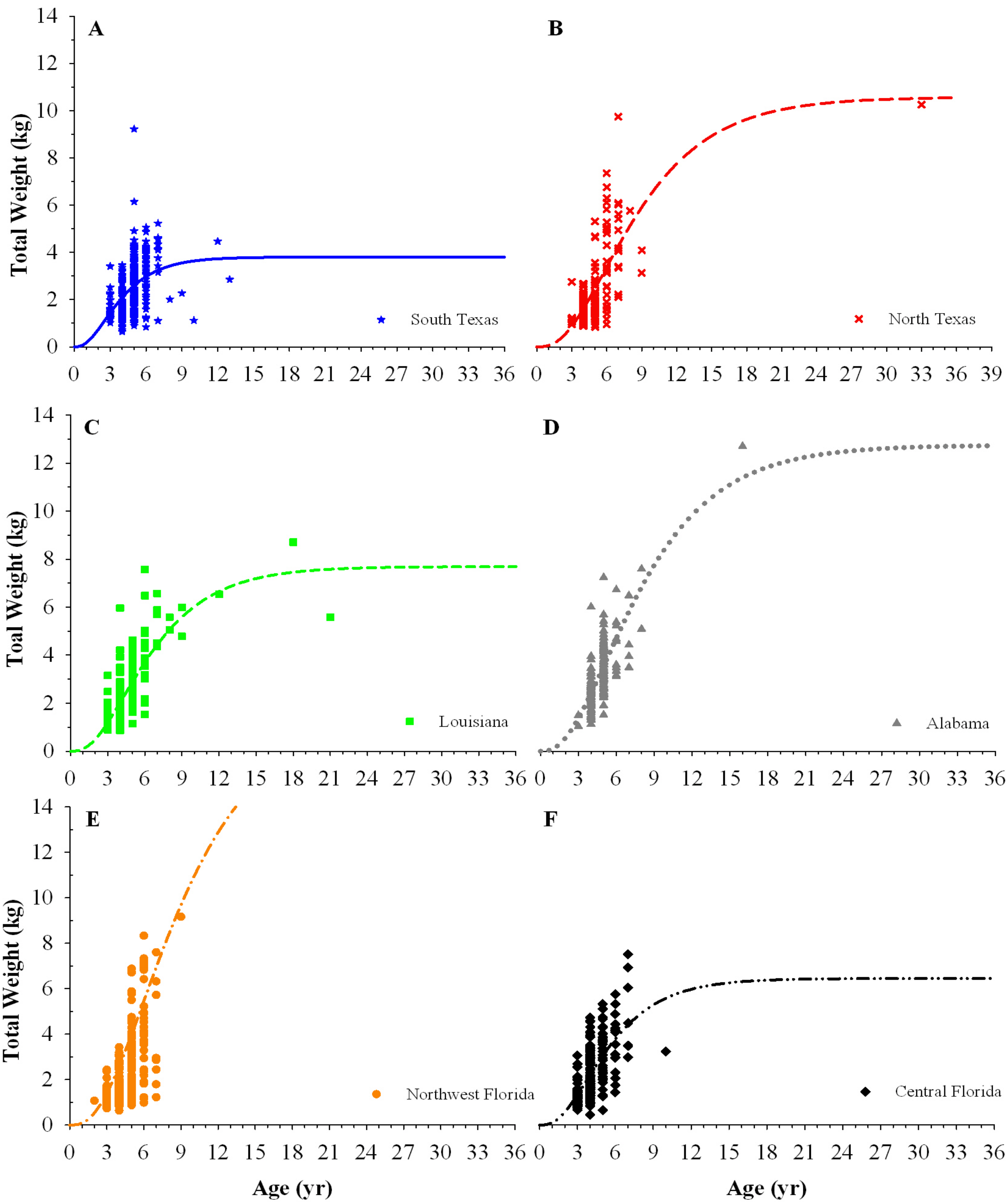

Figure 3.14. Observed total weight at age and von Bertalanffy growth models for red snapper, *Lutjanus campechanus*, from six recreational fishing regions in the Gulf of Mexico: (A) South Texas (n=318), (B) North Texas (n=203), (C) Louisiana (n=193), (D) Alabama (n=177), (E) Northwest Florida (n=388), and (F) Central Florida (n=265).

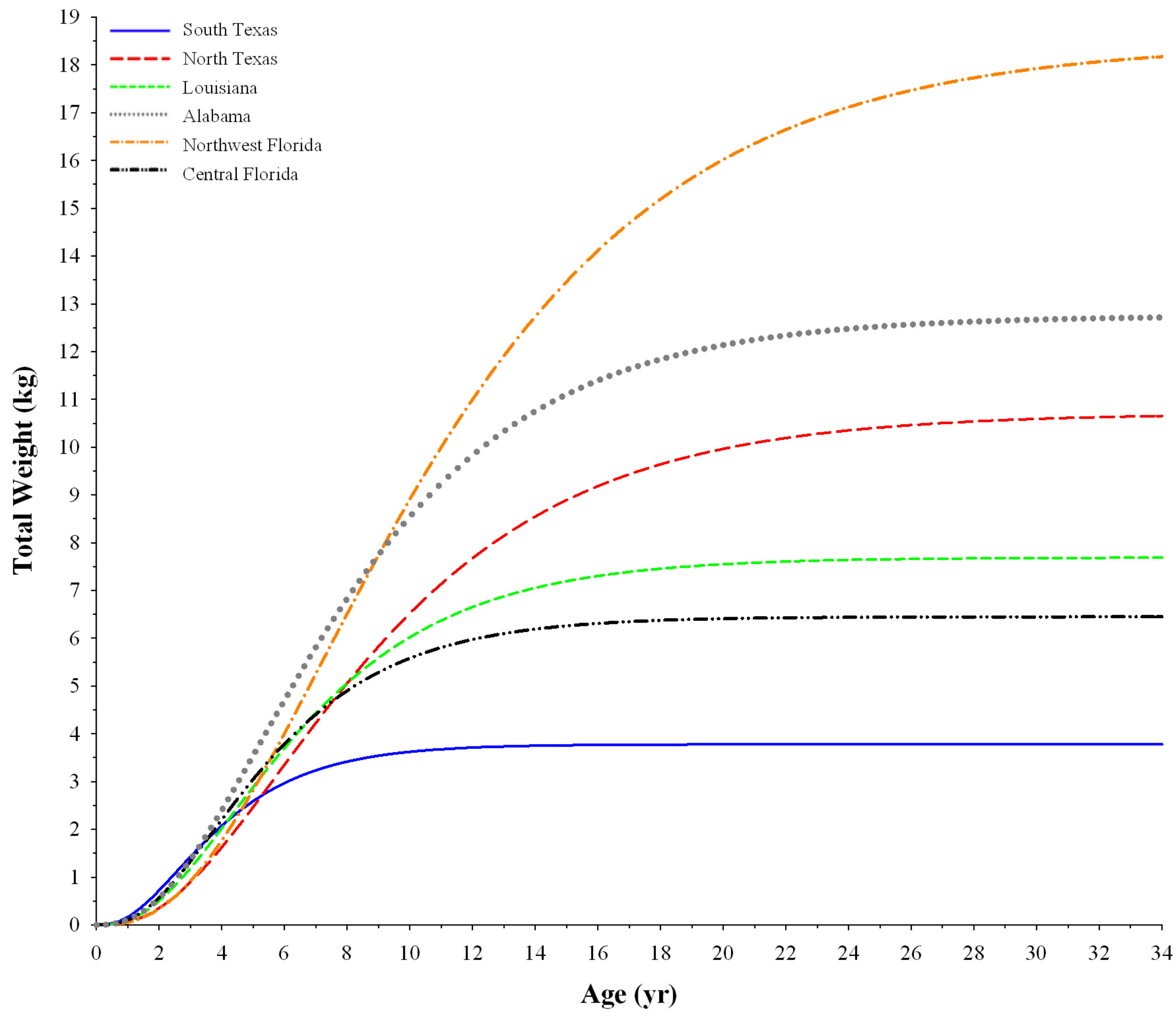

Figure 3.15. Comparative von Bertalanffy growth models for red snapper, *Lutjanus campechanus*, total weight at age from six recreational fishing regions in the Gulf of Mexico: South Texas (n=318), North Texas (n=203), Louisiana (n=193), Alabama (n=177), Northwest Florida (n=388), and Central Florida (n=265).

Table 3.17. Likelihood ratio test p-values for comparing red snapper, *Lutjanus campechanus*, total weight von Bertalanffy growth models and parameters among six recreational fishing regions in the Gulf of Mexico: South Texas (n=318), North Texas (n=203), Louisiana (n=193), Alabama (n=177), Northwest Florida (n=388), and Central Florida (n=265).

	MODEL	**W_∞**	**K**
South Texas - North Texas	<0.0001	<0.0001	<0.0001
South Texas - Louisiana	<0.0001	<0.0001	<0.0001
South Texas - Alabama	<0.0001	<0.0001	<0.0001
South Texas - Northwest Florida	<0.0001	<0.0001	<0.0001
South Texas - Central Florida	<0.0001	<0.0001	0.0001
North Texas - Louisiana	<0.0001	<0.0001	<0.0001
North Texas - Alabama	<0.0001	0.0190	0.4443
North Texas - Northwest Florida	<0.0001	0.0101	0.0441
North Texas - Central Florida	<0.0001	<0.0001	<0.0001
Louisiana - Alabama	<0.0001	<0.0001	0.0011
Louisiana - Northwest Florida	<0.0001	<0.0001	<0.0001
Louisiana - Central Florida	<0.0001	0.0135	0.0053
Alabama - Northwest Florida	<0.0001	0.0007	<0.0001
Alabama - Central Florida	0.0001	0.0003	0.0003
Northwest Florida - Central Florida	<0.0001	<0.0001	<0.0001

3.4 Discussion

3.4.1 Red Snapper Age Structure

Across all of the regions, red snapper were young (mean age of 4.51 ± 0.03 yr), and exhibited a truncated age structure with few fish older than six years (3.95% of the samples) and less than 1% older than ten years. The dominant age classes observed (85.84% of the samples) are thought to represent the strong recruitment from 2004, 2005 and 2006 (SEDAR 2009; Cowan 2011). The oldest red snapper collected in this study was 33 years old, which is twenty years younger than the oldest reported red snapper in the GOM (Wilson and Nieland 2001; Mitchell et al. 2004; Allman and Fitzhugh 2007). Several reports of red snapper sampled in the late 1990s and early 2000s confirm the longevity of red snapper and report a higher prevalence of older red snapper than is observed in this study (Patterson et al. 2001; Wilson and Nieland 2001; Allman et al. 2002; Fischer et al. 2004; Mitchell et al. 2004; Allman and Fitzhugh 2007). Ten years ago, Fischer et al. (2004) reported 10% of red snapper examined from the recreational catches of Texas, Louisiana and Alabama were older than 6 years of age, which is more double the occurrence of old red snapper in this study (4%). However, Fischer et al. (2004) had a much larger sample size (n=5035) and, unlike this study, they included red snapper from recreational fishing tournaments, where anglers specifically target large fish.

Recent analyses of the GOM red snapper fisheries report a decline in frequency of larger, older red snapper in the catches (Allman and Fitzhugh 2007; Nieland et al. 2007; Nieland et al. 2007) and the most recent stock assessments indicate that red snapper older than 8 years are rarely caught in the GOM recreational and commercial red snapper fisheries (SEDAR 2005; SEDAR 2009). The absence of truly old red snapper in this study could be attributable to the intense overfishing that occurred during the mid to late 1900s, which brought the GOM red snapper stock to its most depleted state in the late 1980s and early 1990s (SEDAR 2009; Cowan et al. 2010). This large decrease in spawning stock biomass severely hindered the success and survivorship of subsequent year classes, producing only two dominant year classes between 1980 and 2000 (Allman and Fitzhugh 2007), and is a plausible reason why there is a scarcity of older fish (>15 yr) observed today (Allman and Fitzhugh 2007; Nieland et al. 2007; Nieland et al. 2007; SEDAR 2009).

However, it has also been documented that the GOM recreational red snapper fishery typically catches younger red snapper compared to the commercial fisheries (SEDAR 2005; Allman and Fitzhugh 2007). Allman and Fitzhugh (2007) found that from 1991-2002 the recreational fishery (not including tournaments) selected for the youngest red snapper with a mean of 3.2 years compared to the mean of 4.1 years for the commercial handline fishery and 7.8 years for the commercial longline fishery. These differences may reflect gear selectivity, depths fished, geographic location, fish behavior, and habitat-preference (Wilson and Nieland 2001; Allman et al. 2002; Nieland and Wilson 2003; Mitchell et al. 2004). Several studies have emphasized that the age-specific habitat preferences of red snapper may influence the age classes captured in the various fisheries and thus it may be requisite for future management strategies to take this variability into account (Render 1995; Workman et al. 2002; Nieland and Wilson 2003; Wells et al. 2008). Red snapper exhibit a strong affinity for structure and undergo an ontogenetic habitat shift during their first several years of life, moving from low-relief habitats to habitats with higher relief and greater complexity, that are usually in deeper waters (Render 1995; Workman et al. 2002; Nieland and Wilson 2003; Szedlmayer and Lee 2004; Geary et al. 2007; Wells et al. 2008). In the northwestern GOM, it has been hypothesized that older red snapper (>6-8 years) become less reef-associated once they reach a size threshold that allows them to escape predation and emigrate away from artificial structures such as oil and gas platforms to alternative habitats (Render 1995; Nieland and Wilson 2003; Mitchell et al. 2004).

Differences in the age-structure of the catch of various fisheries may also be a function of fishing practices. Typically, recreational fishermen are limited by trip time, bag limits, and seasonal closures unlike commercial handline fishermen who are under an IFQ system and commercial longliners who are restricted to depths greater than 90 m; thus recreational fishermen fish at shallower depths, closer to shore. However, recent stock assessments indicate that red snapper older than 8 years are rarely caught in both the recreational and commercial red snapper fisheries (SEDAR 2009).

The predominance of small, young red snapper in this study reflects the recent decline in size at age of red snapper (Nieland et al. 2007) as well as the age truncation of the population (Allman and Fitzhugh 2007) due to overfishing (Berkeley et al. 2004). Several compensatory responses to fishing pressure, including age truncation, faster growth, and early maturation, have been noted in the GOM red snapper stock (Fischer et al. 2004; Jackson et al. 2007; Nieland et al. 2007; Allman et al. 2009) and are present in this study. Removal of the largest and oldest fish results in a truncated age distribution and can have substantial negative effects on the population's recovery (Leaman and Beamish 1984; Trippel et al. 1997). Because fecundity increases with fish size and age, and longevity extends reproduction across a long period of time, truncating the age distribution of the stock decreases its reproductive capabilities and could impose severe limitations on population recovery (Leaman and Beamish 1984; Trippel et al. 1997; Berkeley et al. 2004; Berkeley et al. 2004; Palumbi 2004). Other documented maladaptive responses to fishing pressure include earlier maturation (juvenescence), smaller egg volume, lower larval survival, and lower fecundity (Trippel 1995; Walsh et al. 2006); all of which greatly reduce the population's capacity for recovery.

3.4.2 Demographic Differences in GOM Red Snapper

In the past decade, a significant difference between the age-frequency distributions and size-at-age of red snapper across the northern GOM has also been observed (Allman et al. 2002; Fischer 2002; Fischer et al. 2004; Allman and Fitzhugh 2007). Fischer et al. (2004) found that Texas red snapper (sampled from the recreational catch) reached a smaller maximum size at a faster rate than Louisiana and Alabama red snapper, with the majority of Texas red snapper under 3 yr of age and 375 mm fork length. Corresponding to Fischer et al's findings, Saillant and Gold (2006) found the population structure of red snapper to vary across the GOM, indicating different "demographic stocks" with dramatically different effective population sizes (Saillant and Gold 2006). Fischer et al. (2004) hypothesized that these findings may be due to a combination of differing environmental conditions and management regimes across the northern GOM, as well as the type of recreational fishing vessels (headboats in Texas versus charter boats in Louisiana and Alabama) and the disproportionately high discard-to-landing ratio reported for headboats in Texas. Several fishery dependent and fishery independent studies have also found differences in the age structure of red snapper landings across the GOM during the 1990s and 2000s, with older, larger red snapper occurring more frequently in the western GOM (Allman et al. 2002; Mitchell et al. 2004; Allman and Fitzhugh 2007; SEDAR 2009).

This current study supports these reports of a geographic pattern in age structure of red snapper across the GOM. Both of the Florida regions sampled had significantly younger and smaller red snapper than the north-central and western GOM regions. However, as Allman and Fitzhugh (2007) observed consistent gulf-wide year-class patterns, this study also found evidence of strong year-classes (2004, 2005 and 2006) in all six regions. This combination of demographic differences and gulf-wide year-class consistency supports recent findings that red snapper across the GOM form a metapopulation (or network) of semi-isolated assemblages, which are demographically distinct but also highly influenced by migration between assemblages (Gold and Saillant 2007). In a review of red snapper movement and distribution studies, Patterson (2007) concluded that GOM red snapper should be considered a metapopulation because across the GOM there exist distinct subunits with discrete demographics and vital rates, yet dispersal mechanisms exist, including the capability of red snapper to move large distances (Patterson et al. 2001; Patterson and Cowan 2003; Diamond et al. 2007; Strelcheck et al. 2007) as well as relocation by hurricane disturbance (Watterson et al. 1998; Turpin and Bortone 2002; Patterson and Cowan 2003), that allow for mixing among the subunits.

The size and age frequency distributions, von Bertalanffy growth models, and size-at-age models from this study indicate significant demographic differences in red snapper across the GOM. Small, fast-growing individuals dominated the recreational catches of South Texas, Northwest Florida and Central Florida, whereas larger, slower growing red snapper constituted the majority of the Alabama and Louisiana recreational catches, thus supporting the findings of Fischer et al. (2004). The catches in the eastern GOM regions were dominated by younger red snapper (70.8% were younger than 5 years, 0.26% were older than 7 years) while the catches in the northern and western GOM had more uniform distributions of the age classes (45.3% and 43.5% were younger than 5 years, respectively) and a slightly larger representation of red snapper older than 7 years (2.1% and 1.7%, respectively). These findings are consistent with those of Mitchell et al. (2004), Allman and Fitzhugh (2007), and SEDAR (2009).

The von Bertalanffy growth models of TL at age estimated in this study indicate differences in the growth of red snapper across the GOM. However, very few old red snapper were observed and thus the von Bertalanffy models may not be representative of each entire subpopulation because the models are strongly determined by the L_∞ estimates, which are derived from larger, older fish (Haddon 2001). This absence of larger, older fish also makes comparisons with previous studies difficult because they were able to include large red snapper from fishing tournaments in their growth models (Patterson et al. 2001; Fischer et al. 2004). Also, very few red snapper under the age of 3 yr were included in this study's samples due to the minimum size limit on the recreational fishery (>406.4 mm TL). Therefore, the von Bertalanffy growth models were forced through $t_0=0$ in order to more accurately predict juvenile growth. Forcing t_0 through zero may increase estimates of *k,* however the *k* estimates from this study were comparable to estimates from previous studies (Patterson et al. 2001; Wilson and Nieland 2001; Fischer et al. 2004). Nonetheless, sample sizes were fairly consistent among the regions, so I was able to statistically compare the growth of red snapper over the age ranges collected.

The von Bertalanffy growth models of TL at age suggest that red snapper from North Texas and Alabama reach significantly larger maximum theoretical total lengths (L_∞) than red snapper from the other four regions. These L_∞ estimates are similar to previously reported maximum lengths for red snapper from Alabama and Louisiana (Render 1995; Patterson et al. 2001; Fischer et al. 2004). However, the L_∞ estimate for Louisiana red snapper was smaller than previous reports (Wilson and Nieland 2001; Fischer et al. 2004; Nieland et al. 2007), possibly reflecting the recent decline in size at age of GOM red snapper (Nieland et al. 2007) and the age truncation of the population (Allman et al. 2009) as seen by the lack of larger, older fish observed. The TL growth models also indicate that red snapper from South Texas and Northwest

Florida reach smaller maximum total lengths than red snapper from the other four regions (Fig 3.13) as well as from previous studies (Fischer et al. 2004; Burns and Brown-Peterson 2006), which is another indication of severe overfishing and age truncation in these two regions. However, it is difficult to obtain accurate estimates of the L_∞ asymptote without many large, old fish. Thus, the L_∞ estimate for the South Texas red snapper appears to have been heavily influenced by the small size of the five fish older than 7 years from that region (Fig 3.12A). Also, the L_∞ estimate for the Northwest Florida red snapper may have been strongly influenced by the large variability in TL at ages 6 and 7 years, along with the extremely small sample size (n=1) of red snapper older than 7 years (Fig 3.12E). It also appears that red snapper are devoting more of their energy as younger fish to reproductive rather than somatic growth, as fish sampled off Louisiana in a companion study are reaching 50% maturity by age 3 (Kulaw, personal communication[2]).

The von Bertalanffy growth models of TL at age also indicate significant differences in the estimated growth coefficients (*k*) among the regions. The South Texas model exhibited a significantly larger *k* than red snapper from all of the other five regions, and is consistent with the faster growth rates reported by Fischer et al. (2004) for Texas red snapper. The second fastest *k* estimates were from the two Florida regions and may be influenced by the dominance of young individuals (only 2 individuals older than 7 years) in the samples from these regions. These fast *k* estimates could also be the result of a compensatory, density-dependent response to overexploitation (Trippel 1995; Rose et al. 2001; Berkeley et al. 2004; Nieland et al. 2007). As previously noted, these faster growth rates may be a result of forcing the models through t_0=0,

[2] Kulaw, D. K. 2011. Louisiana State University. Department of Oceanography and Coastal Sciences.

however, Fischer et al. (2004) also sampled the recreational red snapper fishery and forced their von Bertalanffy models through $t_0=0$, obtaining similar *k* estimates to those found in this study.

Unlike the South Texas red snapper, the von Bertalanffy model of North Texas red snapper is indicative of slower growth in this region. Slower growth rates can also be indicative of overfishing, for instance if fishermen continuously remove the rapidly growth fish (the fish that meet minimum size regulations faster and large, fast growing trophy fish), they are inadvertently selecting for the survival of slow-growing individuals (Trippel et al. 1997; Zhao et al. 1997; Walsh et al. 2006). Red snapper from northern Texas appear to be more similar to red snapper in northern GOM regions (Louisiana and Alabama) than southern Texas red snapper. These findings are consistent with reports of significant post-settlement movement of red snapper between the northern and western GOM and indications from otolith microchemistry analysis and larval transport studies that recruitment in the western GOM is subsidized by recruits from Louisiana (Cowan et al. 2002; Patterson 2007; Patterson et al. 2008; Johnson et al. 2009; Sluis, personal communication[1]). Similarities were also observed between the Louisiana and Central Florida red snapper, which may be indicative of connectivity of these regions by the offshore currents that flow clockwise along the outer continental shelf, potentially transporting larvae and adults (Ohlmann and Niiler 2005; Johnson et al. 2009).

The differences between the southern and northern Texas red snapper may also be attributable to mixing of the red snapper stocks between southern Texas and Mexico. The Mexican red snapper population is severely overfished (Monroy-Garcia et al. 2002) and the predominance of small, fast-growing individuals in a population is a sign of juvenescence and usually indicative of overfishing (Trippel 1995; Nieland et al. 2007). To date, no direct comparisons of red snapper age and growth from Mexican and U.S. waters have been made.

However, an ongoing study using otolith microchemistry is examining the use of chemical signatures for natal origins of red snapper as well as the connectivity of the red snapper stocks in the western and southern GOM (Sluis, personal communication[1]).

The von Bertalanffy growth models of red snapper TW at age also indicate differences in growth rates (*k* estimates) and maximum theoretical total weights (W_∞) among the regions. Similar to the von Bertalanffy TL at age models, the South Texas red snapper TW model exhibits the fastest growth coefficient (*k*) and reaches the smallest maximum theoretical total weight (W_∞), while the North Texas model exhibits the slowest *k*. The estimates of *k* from the von Bertalanffy TW models were similar among the north-central and northwestern GOM regions, supporting previous reports of similar growth parameters between Louisiana and Alabama red snapper (Patterson et al. 2001; Fischer et al. 2004). However, estimates of W_∞ for Louisiana and Alabama red snapper were smaller than previously reported (Fischer et al. 2004), which could be an artifact of the absence of larger, older fish in this study and the presence of large tournament fish in the previous study, or it may demonstrate the recent decline in size at age of red snapper across the GOM (Nieland et al. 2007). Unlike the von Bertalanffy growth model of TL at age for red snapper from Northwest Florida, the TW model for this region exhibited the slowest *k* and largest W_∞ estimates. These estimates could be due to the absence of larger, older red snapper in the samples from Northwest Florida, which can result in the curve failing to 'heal-over' and the model estimating a larger asymptote, as well as the high variability in TW at ages 5 to 7 years (Fig 3.14E).

3.4.3 Possible Causes for Region-Specific Differences

Demographic variation in size and growth rates may result from differences in environmental factors, fishing pressure, habitat-preference, and management regimes among the regions, as well as localized population responses to fishing pressure. Numerous environmental differences, including availability of suitable habitat, productivity of the surrounding ecosystem, and community structure, could contribute to the demographic dissimilarity among the regions.

The continental shelf across the GOM is predominantly soft bottom, with a scattering of low-relief hard bottom and numerous artificial structures, and lined with shelf-edge banks. Thus, habitat complexity and patchiness varies greatly throughout the GOM. The amount and suitability of preferred habitat may affect the observed age and growth differences for red snapper in this study. The western GOM is predominantly soft bottom (clay and sand) with a scattering of natural hard bottom, oil and gas platforms, and artificial reefs. The northern GOM is similar with a scattering of low-relief outcrops and the shelf edge is lined with natural hard-bottom bedrock banks (Rezak et al. 1985). The northern GOM also has the largest artificial reef system in the world made of oil and gas platforms off Louisiana (Pulsipher et al. 2001) and an extensive artificial reef network of smaller reefs off Alabama (Minton and Heath 1998). The eastern GOM differs from the northern and western GOM with sandier sediments, a higher proportion of natural hard-bottom, and a wider, shallower shelf devoid of oil and gas platforms.

Differing amounts of nutrient availability, primary productivity, and secondary productivity among the regions may also be influencing the growth differences in red snapper among the regions. The coastal waters of the north-central and northeastern GOM are river-dominated systems that experience high levels of nutrient-rich freshwater discharge and sediment inputs from a suite of rivers including Mobile Bay and the Mississippi-Atchafalaya rivers (Milliman and Meade 1983; VERSAR 2009). The Mississippi River inputs increased nutrient levels and sediments onto Louisiana’s continental shelf, and the productive, nutrient-rich waters of the river’s plume have been shown to influence fishery production through increased growth rates when compared to other regions of the GOM (DeVries et al. 1990; Grimes 2001). Fischer et al. (2004) speculated that the fertile waters of the north-central GOM are more conducive to faster growth of red snapper in Louisiana and Alabama than in the western GOM. While the fastest growth rates estimated in this study were not from Louisiana, the estimates for growth of Louisiana red snapper were slightly larger than those for North Texas and Alabama red snapper.

Age-specific habitat preference may also play a role in the differences observed in this study. Juvenile red snapper spend their first several years of life on a variety of habitats on the inner-shelf, settling on shell habitats, small inshore reefs, sand habitat, and low relief structure, depending on what habitat is available in the region (Workman and Foster 1994; Szedlmayer and Howe 1997; Szedlmayer and Conti 1999; Workman et al. 2002; Geary et al. 2007; Wells et al. 2008). Red snapper undergo an ontogenetic habitat shift, moving to higher-relief habitat with increasing size and age, and adults show a strong affinity for structure throughout the GOM (Nielson 1992; Szedlmayer and Shipp 1994; Gledhill 2001; Nieland and Wilson 2003; Wells and Cowan 2007). McCawley and Cowan (2007) suggest that red snapper's affinity for reefs and structured habitats is a behavioral preference, most likely related to the refuge provided by the structure and the gregarious nature of the species, not related to foraging opportunities because the majority of their diets come from non-reef associated benthic fauna and fish. Several studies have documented the opportunistic feeding habits of red snapper, showing that their prey come from various habitats, including benthic sand and mud habitats, the water column, and a small portion from reefs or hard bottom habitats (Gallaway et al. 1981; Szedlmayer and Lee 2004; McCawley and Cowan 2007; Wells et al. 2008). Therefore, regional differences in red snapper growth may be attributable to the quantity and quality of the prey available among the different habitats.

It is also important to note that red snapper have never been uniformly distributed across the GOM (SEDAR 2005; Porch et al. 2007). The GOM red snapper fishery began in the northeastern GOM in the 1800s and was heavily exploited by the end of the 19th century, forcing fishermen to search for red snapper further south and west, resulting in heavy exploitation of the Mexican red snapper stock (Porch et al. 2007). Commercial landings data over the past century indicate a recent shift in the center of abundance of red snapper from the northeastern GOM off Alabama and Northwest Florida to the northwestern GOM off Louisiana (Porch et al. 2007). The prolonged period of heavy exploitation and near collapse of the fishery in the eastern GOM have had severe impacts on the stock size as well as the size and age structure of red snapper in Florida waters, which has only recently started showing signs of recovery (SEDAR 2009). The distribution of fishing sectors in the GOM has also shifted over time with the center of abundance of red snapper; there is a higher proportion of the commercial landings in the western GOM and the majority of the recreational landings occur in the eastern GOM (SEDAR 2009). Thus, the uneven distribution of the fishing sectors combined with their differing management plans (quotas, minimum size limits, trip/bag limits) may also significantly influence the formation of demographic red snapper stocks in the GOM.

3.5 Conclusions

This study documented the truncated age structure of the red snapper recreational catches as well as demographic differences in red snapper size and age frequencies and growth parameters across six recreational fishing regions of the GOM. Small, fast-growing individuals dominated the recreational catches of South Texas, Northwest Florida and Central Florida, whereas larger, slower growing red snapper constituted the majority of the Alabama and Louisiana recreational catches. Also, both of the Florida regions' catches were comprised of significantly younger red snapper than the red snapper catches in the north-central and western GOM regions.

These results are consistent with previous reports that red snapper from Texas grow at a faster rate and reach a smaller maximum size than red snapper from Louisiana and Alabama (Fischer et al. 2004). Although the demographic differences in red snapper age and growth parameters that exist across the GOM are likely attributable to fishing pressure and environmental differences, no definitive conclusion as to the driving factor can be made at this time. However, it is evident that differences in red snapper population demographics exist across the GOM. Implications of these differences and the theory that red snapper form a metapopulation in the GOM should be considered in future stock assessments and management decisions.

These results also indicate that there is a decline in the frequency of larger, older red snapper in the recreational catches. The most recent red snapper stock assessment suggests that red snapper in the western GOM are beginning to recover from overfishing (SEDAR 2009), and it is expected that as the stock rebuilds, there will be a shift to an older age structure (Allman and Fitzhugh 2007; SEDAR 2009). While an increase in red snapper biomass has been observed in the fisheries, an age shift is not readily apparent in this study, the stock assessments, and other recent studies (Allman and Fitzhugh 2007; SEDAR 2009). Identification and protection of the strong year classes will allow for the stock to recover and eliminate the severely truncated age structure as more fish reach maximum spawning potential, which is crucial for stock recovery given that reproductive success increases with maternal age (Berkeley et al. 2004; Palumbi 2004; Walsh et al. 2006).

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CHAPTER 4: SUMMARY AND CONCLUSIONS

4.1 Summary

The overall goal of my research was to examine the age and growth of red snapper (*Lutjanus campechanus*) among different habitats and regions in the Gulf of Mexico (GOM). The GOM red snapper stock has been exploited since the mid 1800s; yet it is still one of the most economically important fisheries in the GOM. The GOM red snapper population has been declining since the 1970s and under intense management as a unit stock since the late 1980s (Goodyear 1995; SEDAR 2005; GMFMC 2007; Porch 2007; SEDAR 2009). Results of the 2009 stock assessment update indicate that although the GOM red snapper stock is overfished, it is perhaps no longer undergoing overfishing in the western GOM, and the current management policy has set a rebuilding plan for stock recovery by 2032 (SEDAR 2009; GMFMC 2010).

To facilitate red snapper recovery, population assessments and management tools are reliant on accurate estimates of vital population rates, such as age structure and growth rate, as well as information concerning the ecological function of specific types of habitats across the GOM. Habitat type varies greatly throughout the GOM, and while numerous studies have aged red snapper, no studies have simultaneously compared red snapper age structure and growth rate among standing and toppled oil and gas platforms with natural hard bottom habitats. This research specifically addresses the void in the baseline understanding of red snapper vital rates and helps define biological reference points for this species on natural habitats. This research also addresses the demographic differences noted in the most recent red snapper stock assessments (SEDAR 2005; SEDAR 2009) and scientific literature (Fischer et al. 2004; Allman and Fitzhugh 2007; Patterson 2007), and can be used to further evaluate the need for management sub-units.

In Chapter 2, I examined differences in red snapper size and age structure and growth rate from offshore natural habitats (shelf-edge banks), standing oil and gas platforms, and toppled oil and gas platforms on Louisiana's outer continental shelf. Across all habitats, red snapper were young and exhibited a truncated age structure with less than 1% of the fish older than ten years of age. Red snapper from the shelf-edge banks were significantly smaller at age than red snapper from the standing and toppled platforms. Red snapper from the shelf-edge banks also exhibited a slower growth rate and smaller maximum size than red snapper from the standing and toppled platforms, as well as from previous reports. However, it is interesting to note that the shelf-edge banks appear to support a higher predominance of relatively older (>6 yr) red snapper compared to the standing and toppled platforms. Habitat-specific differences documented in this study reflect the phenotypic plasticity found in the GOM red snapper stock, which can be intensified by varying exploitation rates, diet composition and habitat preference. This study is also consistent with the recent NMFS report that a large, offshore or deepwater cryptic biomass of red snapper does not exist in the northern GOM (SEDAR 2009).

In Chapter 3, I examined the size and age structure, growth models, and size-at-age of red snapper from the recreational catches of six regions of the GOM (South Texas, North Texas, Louisiana, Alabama, Northwest Florida, Central Florida). Overall, red snapper were young (mean age of 4.51 ± 0.03 years) and exhibited a truncated age structure with few fish older than six years (3.95% of the samples) and less than 1% older than ten years (0.41%). Small, fast-growing individuals dominated the recreational catches from South Texas, Northwest Florida and Central Florida, whereas larger, slower growing red snapper constituted the majority of the Alabama and Louisiana recreational catches. Also, the recreational catches of red snapper in the eastern regions (North and Central Florida) were comprised of younger red snapper than in the catches from the north-central and western GOM regions. These results are consistent with previous reports that red snapper from Texas grow at a faster rate and reach a smaller maximum size than red snapper from Louisiana and Alabama (Fischer et al. 2004). These results also indicate that there is a decline in the frequency of larger, older red snapper in recreational catches. Although demographic differences in red snapper age and size structure and growth rate that exist across the GOM are likely attributable to fishing pressure and environmental differences, no definitive conclusion as to the driving factor can be made at this time.

4.2 Age Structure of GOM Red Snapper

Chapters 2 and 3 documented the truncated age structure of GOM red snapper (combined mean age 4.44 yr with 1.5% older than 7 yr). The absence of truly old red snapper in both of these chapters could be attributable to the intense overfishing that occurred during the mid to late 1900s, which brought the GOM red snapper stock to its most depleted state in the late 1980s and early 1990s (SEDAR 2009; Cowan et al. 2010). This large decrease in spawning stock biomass severely hindered the success and survivorship of subsequent year classes, producing only two dominant year classes between 1980 and 2000 (Allman and Fitzhugh 2007), and is a plausible reason why there is a scarcity of older fish (>15 yr) observed today (Allman and Fitzhugh 2007; Nieland et al. 2007; Nieland et al. 2007; SEDAR 2009). Also, samples indicate that relatively few members of these strong year classes are likely to have survived to ages of maximum spawning potential.

Red snapper exhibit a periodic life history strategy distinguished by delayed maturation, longevity, high fecundity, synchronous spawning, and small egg size (Winemiller and Rose 1992; Winemiller and Rose 1993; Render 1995; Woods et al. 2003; Cowan et al. 2010). Their bet-hedging reproductive strategy and protracted spawning seasons are reported to produce a strong year class every 5-10 yr (Allman and Fitzhugh 2007). When combined with their longevity, this periodic occurrence of strong year classes is sufficient to maintain a stable population biomass under modest harvesting (Cowan et al. 2010). However, when under prolonged overfishing, periodic strategists are initially resistant to overexploitation but take a much longer time to recover due to the infrequency of strong year classes (Winemiller and Rose 1992; Secor 2000; Cowan et al. 2010). Thus, identification and protection of the strong year classes are requisite to allow the stock to recover. Protection of the strong year classes will allow more fish to reach maximum spawning potential, which is crucial for stock recovery given that reproductive success (increased fecundity and larval survivorship) increases with maternal age (Berkeley et al. 2004; Palumbi 2004; Walsh et al. 2006).

4.3 Fisheries Management Implications

The most recent red snapper stock assessment suggests that red snapper in the western GOM are beginning to recover from overfishing (SEDAR 2009), and it is expected that as the stock rebuilds, there will be a shift to an older age structure (Allman and Fitzhugh 2007; SEDAR 2009). While an increase in red snapper biomass has been observed in the fisheries, an age shift is not readily apparent in this study, the stock assessments, and other recent studies (Allman and Fitzhugh 2007; Nieland et al. 2007; SEDAR 2009). The truncated age structure and prevalence of faster growth rates of red snapper throughout the GOM are compensatory responses to overfishing that could severely hinder the population's ability to recover. Fisheries managers should consider these maladaptive responses in the stock when evaluating future assessments and management options, as well as the potential stock responses associated with future management options. As previously discussed, identification and protection of the strong year-classes is necessary in order to 1) allow more red snapper to reach maximum spawning potential and ensure the success of future year-classes, and 2) repopulate the older age classes to eliminate the severely truncated age structure. It has been recommended that managers regularly review the red snapper rebuilding plan to include advances in scientific research and adapt the current policy in order to address the short-term directions while not losing site of the long-term goal (SEDAR 2005; Strelcheck and Hood 2007). Thus, to prevent habitat- and region-specific overfishing and promote stock recovery, the differences observed in this study should be weighed when evaluating future stock assessments and management decisions and delineating essential fish habitat in the northern GOM.

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Courtney Rose Saari was born in Rhode Island in August of 1986. She grew up with a younger brother in North Kingstown, Rhode Island, and graduated from North Kingstown Senior High School in 2004. She attended Eckerd College in St. Petersburg, Florida, and graduated with a Bachelor of Science with honors in marine science with a biology concentration in 2008. During her tenure at Eckerd College, Courtney participated in the Eckerd College Ford Scholar Apprenticeship Program and the Eckerd College Natural Sciences Summer Research Program (NSSRP). Courtney was also awarded a NOAA Hollings Scholarship and Internship in 2006. Courtney completed a rigorous undergraduate research thesis in 2007, receiving an A with honors. Her thesis was titled "Environmental Effects on the Germination of the Central Florida Submerged Macrophyte *Vallisneria americana* (wild celery)." During her senior year and the summer following graduation, Courtney worked as research staff in the Habitat Research and Restoration division at the Florida Fish and Wildlife Research Institute under the direction of Dr. Paul Carlson. In August 2008, Courtney moved to Baton Rouge, Louisiana, to begin her graduate work under the supervision of Dr. James H. Cowan Jr. in the Department of Oceanography and Coastal Sciences within the School of the Coast and Environment at Louisiana State University. She defended her thesis on June 24, 2011 and was awarded the degree of Master of Science in Oceanography and Coastal Sciences on August 5, 2011.